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THE TRANSACTIONS OF THE ZOOLOGICAL SOCIETY OF LONDON

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THE FOOD OF NON-CICHLID FISHES IN THE LAKE VICTORIA BASIN, WITH REMARKS ON THEIR EVOLUTION AND ADAPTATION TO LACUSTRINE CONDITIONS

BY

PHILIP S. CORBET

*East African Fisheries Research Organization, Jinja, Uganda**

[Accepted 10th May 1960]

(With 20 figures in the text)

The food of twenty-six species of non-cichlid fishes in the Lake Victoria basin is described. Most species, for which data were sufficient to show this, are facultative feeders, their food being determined by their size, their feeding grounds, and the age of the moon. The size of an organism and its position in the aquatic environment usually determine its importance as prey, and this is considered a reason why so many fishes in the lake are insectivorous. Only three species of non-cichlid are extensively piscivorous : these feed heavily on *Haplochromis*, slightly on *Engraulicypris*, and hardly at all on *Tilapia*. Several birds and fishes feed on *Engraulicypris*, but otherwise there are few natural predators of non-cichlids. Ontogenetic changes in feeding behaviour of *Mormyrus kannume* and *Bagrus docmac* support the hypothesis (recently confirmed for *B. docmac*) that in the lake juveniles of these two species live on rocky shores. The evolutionary stages involved in the colonization of lakes from rivers are discussed, with particular reference to breeding habits and food. The non-cichlids in Lake Victoria are considered not to have progressed far towards becoming adapted to a lacustrine environment.

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* Present address : Virus Research Institute, P.O. Box 49, Entebbe, Uganda.

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INTRODUCTION

Until recently, no special study has been made of the food of the non-cichlid fishes in Lake Victoria and its associated rivers. Since the first general survey of fisheries in the lake (Graham, 1929), general observations have been published on the food of non-cichlids (E.A.F.R.O., 1949–53) but these have been incidental to wider programmes of work, and necessarily on a small scale. More recently, attention has been paid to the food of *Mormyrus kannume** (Macdonald, 1956 ; Corbet, 1957 b), but from the point of view of the biology of its prey, rather than of its own feeding behaviour. In addition certain fishes in the Victoria Nile have been studied with the particular aim of assessing the effects of DDT on their feeding habits (Corbet, 1958 a).

There are several reasons why it is particularly desirable that information on the food of non-cichlids should be made available as soon as possible. Apart from the general contribution it must make to a clearer understanding of the ecology of a complex and interesting environment, such information has long been required to clarify debate concerning the effective predators of *Tilapia*. Furthermore, the progressive reduction of stocks of these favoured food-fishes by the ever-increasing fishing effort (see E.A.F.R.O. 1954/55 and Garrod, 1957 b), is causing greater attention to be paid to other species of potential economic value. And now that the introduction of large predatory fishes into Lake Victoria is receiving serious consideration, the need for accurate data becomes even more important, since without a firm knowledge of the feeding habits of the resident species, it is impossible to make a useful prediction of the results such introductions are likely to have, or to know the extent to which the existing resources are being utilized.

* The specific name for each non-cichlid fish is given with its authority at the head of the section devoted to that species.

The work described here deals with all non-cichlid species known from Lake Victoria and its associated rivers for which specimens or records were available. Amongst the Cichlidae, the two indigenous species of *Tilapia*, *T. variabilis* Boulenger and *T. esculenta* Graham, are known to feed mainly on phytoplankton, and on epiphytic and epilithic algae (see Fish, 1951, 1955 ; Greenwood, 1953), whereas the remainder, comprising the *Haplochromis* species flock, exhibit a wide variety of feeding habits which has provided the basis for an evolutionary classification of the group (Greenwood, 1951). Accounts have already been published of the food of certain species (Greenwood, 1954, 1956 b, 1956 d, 1957 a). The group has shown extensive adaptive radiation in this respect, and includes algal grazers as well as species feeding on insects, molluscs and fishes. *Haplochromis* are therefore potential competitors with non-cichlids for most main types of food.

It is necessary to mention briefly certain features of Lake Victoria and its fishes in order that the problems inherent in the present study may be appreciated.

(1) The present lake was formed relatively recently, during the Pleistocene era (see Wayland, 1931).

(2) The lake now comprises a wide variety of contrasting habitats (see E.A.F.R.O., 1951).

(3) It is believed that the fish fauna was derived from nearby rivers (see Greenwood, 1951).

(4) Many species of fish in the lake make annual or possibly more frequent excursions into affluent rivers to breed (see Whitehead, 1959).

(5) Within the lake itself most fishes range and feed over a wide variety of substrata.

A consideration of these features makes it clear that Lake Victoria and its associated rivers should be treated together in such a study, but that, at the same time, strict allowance should be made for the type of bottom over which a fish has been feeding. Furthermore, the fact that different species of fishes, particularly Mormyridae, often feed on the same wide range of organisms, means that any differences between the food of related species are likely to be of a subtle nature. It follows that large numbers of fishes must be examined and that a quantitative treatment of the results is essential. This becomes even more obvious when it is recalled that allowance must also be made for the size of fish, and for the phase of the moon, which in Lake Victoria is known to affect the food eaten by *Mormyrus kannume* (Macdonald, 1956) and other fishes (Corbet, 1957 b). During the course of the work it became clear that ordinary methods of treatment would be inadequate, but that, on the other hand, the records were ideally suited for Hollerith analysis.

In the present work Hollerith analysis was used for the fourteen species whose numbers warranted it, and in this way over 8,000 of a total of some 9,000 records were dealt with. After the initial labour of coding, punching and checking the cards, it was possible to obtain in a few hours information which otherwise would have taken many months of excessive labour to extract. Furthermore, once punched, the cards remain permanently available to yield such additional information as may be required of them. From this point of

view, the results presented in this paper represent no more than a preliminary study, since there undoubtedly exist many questions which further analyses would answer. A brief account of the procedure adopted will be given in a subsequent section.

MATERIAL

The fishes examined were obtained as described below.

Lake Victoria

Material came from the northern shores of the lake—between Bukoba, Tanganyika to the west, and Kisumu, Kenya, to the east. Most fishes were caught in gill-nets set by E.A.F.R.O., in or near Napoleon Gulf. These nets were set in the afternoon and lifted early the following morning. Thus most of the fishes were caught at night, probably soon after sunset (E.A.F.R.O., unpublished), and remained in the nets until dawn. Of the remainder, many came from gill-net catches made by native fishermen, and others from catches made with seine-nets or, occasionally, explosives.

Three types of habitat have been recognized. These have been distinguished on the basis of the bottom deposits which, so far as could be ascertained, predominated at each site and up to about 400 metres away from it. The classification of bottom deposits was as follows :

HARD : sand, gravel or rock.

SOFT : mud, silt, humus or clay.

MIXED : hard and soft facies combined.

There are several other variable features on which a habitat classification might be based (e.g. depth, vegetation, or type of nearest shoreline), but the one selected seemed to conform best with the observed distribution of the invertebrate fauna. It must be emphasized, however, that until we possess detailed knowledge of the ecology of the food organisms and of the extent of movements of the fishes, such a classification can only be regarded, at best, as provisional.

Lakeside swamp : some material, particularly of young lungfish, *Protopterus aethiopicus*, was obtained when a marginal grass swamp near Kirinya, Jinja, was cleared by African labourers. This consisted of a floating mat of grass extending out about 25 m. from the shore into water about 1–2 m. deep over a sandy bottom, and flanked on the lakeside by the customary water-lily zone.

Rivers

Victoria Nile : on several occasions in early 1956, the water level of the river was lowered by a metre or more owing to partial closure of the sluice gates of the Owen Falls Dam, Jinja. At such times, large numbers of fishes were collected by E.A.F.R.O. from temporarily exposed areas of the river bed, 50 to 500 m. below the dam. They were collected by hand or with pond nets. The river bed there consists of large, angular boulders of amphibolite. There is a marginal pocket of swamp containing *Echinochloa* and papyrus on the eastern bank connected with the area sampled.

Other rivers : material was also obtained from two large affluent rivers during March and April 1955 and 1956 when fishes were ascending them in numbers to breed. At such times, fishes frequently have empty stomachs, but as these were the only occasions when some species (e.g. *Schilbe mystus*) could be caught in numbers, it was considered worth while examining large numbers of stomachs. Most fishes were caught by native fishermen. In the Kagera River they were caught by drift-nets, conical fishtraps or long-lines, and in the Nzoia River mainly in ' keks '—barriers of non-return fish-traps built across rivers by local fishermen (see Graham, 1929 ; Whitehead, 1958).

Streams :

A few collections were made by E.A.F.R.O. in a swamp stream near Bugungu, Napoleon Gulf, which arose temporarily after rainfall and flowed into the lake (see Greenwood, 1955 b). At other times it became reduced to a series of small pools.

METHODS

The size of each fish was expressed as the ' total length ', this being the distance from snout to end of caudal fin, and, unless otherwise stated, was recorded to the nearest cm. below.

In species with a well-defined stomach, this was removed separately, the wall cut and the contents removed by scraping the inner mucosa with a spatula. The stomach is the best unit to choose for quantitative purposes, being easily defined, and containing the least digested food. In certain species in which a stomach is not clearly recognizable (e.g. *Protopterus aethiopicus* and *Barbus altianalis radcliffi*), the contents of the whole gut were extracted.

Fish food data based on gut contents are suitable for analysis by a variety of methods. This question will be discussed very briefly here, since it has already been reviewed critically by Hynes (1950). The work of Hynes and others makes it evident that the relative importance (to the fish) of different food items can best be gauged by two methods used in conjunction. The first of these (the " occurrence method ") records the number of stomachs in which a given food item occurred (irrespective of its size or abundance) ; the second records the relative abundance of the food item in relation to volume or weight. With certain reservations, Hynes regarded the " points system " devised by Swynnerton & Worthington (1940) as being the best of these for general purposes. This system awards points to each food item, consideration being given to size and abundance of food items and to fullness of stomach. Hynes observed, however, that in most cases substantially the same results were obtained when any of the recognized methods was used, particularly with respect to the *order of importance* of items, and to a lesser extent with respect to the *actual* occurrence values. It is obvious that results derived from, on the one hand, occurrence, and on the other, volume of food items will differ most when a food item is small. This Hynes was able to demonstrate from the results of Idyll (1942) which recorded *Simulium* larvae as food of two species of *Salmo*.

In the present study two statistics were used. The *occurrence* of food items was recorded, and expressed as a percentage of total stomachs containing recognizable food. It should be noted that this makes occurrence values completely independent of the refinement of classification of food items. The existence of relict food in a stomach remains an insuperable problem and may often be responsible for inflated occurrence values, but even so it does not alter the values for other items.

It was sometimes necessary to distinguish between food organisms which had been eaten by the predator, and those derived indirectly *via* its prey. In nearly all equivocal cases, the principle adopted by Lumsden & Haddow (1946) was followed, it being assumed that a fish large enough to consume say, a *Haplochromis* 5 cm. long, would not purposely feed on small insect larvae—particularly if the *Haplochromis* could itself be recognized as an insectivorous species.

To make allowance for the relative volume of a food item, each was given special recognition if it occupied more than half the volume of food in the stomach. It was then given the status of the *main contents*. This method was probably not so accurate as the points system, and suffered from a subjective element when there was very little food in the stomach. (It was not used if only a trace of food was present.) It appeared, however, to be the method best suited to the conditions under which much of the work had to be done—where large numbers of stomach contents had to be examined rapidly with inferior lighting. Values for main contents have also been expressed as a percentage of total stomachs containing food.

Owing to differential digestion and other factors, it is not possible to identify all stomach contents with equal precision. It follows that recorded figures for occurrence will often fall short of the true values, but that the more comprehensive the category of food, the more accurate are they likely to become. Thus, figures for the occurrence of " fish remains ", will necessarily be more accurate than those recording the occurrence of a *particular kind* of fish. The same principle applies in the cases of insects and molluscs. One way in which I have tried to reduce this error is to give extra weight to values for main contents from larger fishes, since such remains are the most likely to be recognizable. These are expressed as *corrected occurrence values*. In the occurrence tables for each species values have been given as integers if derived from less than 101 observations, and to one decimal place if derived from more than 100. The original notes were translated into code and recorded on I.B.M. punch-cards according to the scheme shown in Table 1. Each I.B.M. card contained 80 vertical columns, each with 10 positions for holes, numbered 0 through 9. After these cards had been checked visually, an accounting machine printed out the information on each one, which enabled a final check to be made before the calculations were begun. This done, the information contained in the first 17 columns was printed on the top of each card with a tabulator machine, so that later the cards could be checked or sorted visually if necessary. For the analysis, sorting and accounting machines were employed. With the former, the cards could be arranged in groups according to species, habitat, size or time of year ; and with the accounting

machine, the serial totals for each of the food-types could be computed for each group. As it soon became clear that it was not going to be possible to demonstrate food changes related to time of year, the only variables studied were habitat, size, and in some cases phase of the moon.

TABLE 1

Punch-card coding for fish-food analysis.

Columns	Item	Key
1, 2	species of fish	Yes
3–6	serial number of individual fish	—
7–9	size of fish in centimetres	—
10–12	index number of place where caught	Yes
13, 14	year and month when caught	Yes
15	stomach with or without food	Yes
16, 17	food-type comprising main contents (if any)	Yes
18	blank	—
19–80	individual food-types	Yes

Individual food-types listed in alphabetical order

Column		Column	
34	Anisoptera larvae	57	Hymenoptera
19	Arthropods	36	*Ictinogomphus* larvae
61	*Bellamya*	20	Insects
40	*Brachythemis* larvae	56	Isoptera
74	Bryozoa	60	*Melanoides*
50	*Caridina*	58	Molluscs
71	Cestoda	52	Nematoda
25	Chaoborid larvae	53	Nematoda, alive
26	Chaoborid larvae, alive	72	Non-cichlids
23	Chironomid adults	77	*Nymphaea* seeds
21	Chironomid larvae	33	Ostracoda
22	Chironomid larvae, alive	80	Pebbles
41	Chironomid pupae	62	Pelecypoda
24	Chironomid pupal breathing organs	64	Pelecypoda, large species
66	Cichlidae	63	Pelecypoda, small species
54	Coleoptera	44	*Phanostoma* larvae
42	Corixidae	37	*Phyllomacromia* larvae
77	Culicine larvae	75	Plants, bitten
45	*Ecnomus* larvae	74	Plants, dead
73	*Engraulicypris*	76	Plants, living
32	Ephemeroptera : adults	51	*Potamon*
29	Ephemeroptera : burrowing larvae	28	*Povilla* adults
31	Ephemeroptera : free-living larvae	27	*Povilla* larvae
65	Fishes	79	Sand grains
78	Flower-buds	55	Terrestrial insects
59	Gastropoda	71	*Tilapia*
67	*Haplochromis*	65	Tipulidae
68	*Haplochromis* : hard bottom spp.	47	Trichoptera adults
70	*Haplochromis* : mixed bottom spp.	45	Trichoptera larvae
69	*Haplochromis* : soft bottom spp.	30	*Tricorythus* larvae
48	Hydracarina	38	*Trithemis* larvae
49	Hydracarina, alive	39	*T. annulata* larvae
46	Hydroptilidae	35	Zygoptera larvae

Size	Insects	Molluscs	Fishes
cm. 3	○○ ○		
3	○ ○○		
3	○○ ○		
8	○ ○		
9	○		
10	○○ ○		
12	○○ ○○		
13	○ ○		
14	○ ○		
16	○ ○○		
23	○ ○ ○		
24	○ ○		
25	○ ○		
26	○○		
27	○○○	○○	
29	○ ○○○	○○	
32	○○	○○	
54	○ ○	○○○○○○	○○○
57	○ ○	○○○○○○	
61	○ ○	○○ ○	○○○
62	○ ○	○○○○○○	
68	○ ○	○○○○○ ○	
70		○○ ○	
73		○○ ○○○	
75		○○○○○○	
77		○○○○○○	
80		○○○○○○	
81		○○○○○○	○○○
86		○○○○○○○	
89		○○○○○○○	
96		○○○○○○	
100		○○ ○	
105		○○○○○○○	
110		○○ ○○ ○	
126		○○ ○	
180		○ ○ ○	

Fig. 1.—*Protopterus aethiopicus*. Scatter diagram showing change of food with size in Lake Victoria. A Hollerith accounting machine can be used to print data in this form, which clearly reveals any trends worth further analysis.

It is appropriate to mention here one respect in which an accounting machine can be used with great benefit in an investigation of this kind. If cards bearing information are arranged in order of size of fish, and then passed through an accounting machine which has been wired to print the results in a certain fashion, the machine produces a scatter diagram capable of revealing changes of food with size. The early possession of such a diagram enables

effort to be concentrated to the most profitable ends, and also obviates much tedious and unnecessary analysis. When codings are being devised for such work, it is advisable to keep this possibility in mind. An example of data printed in this way is given in Fig. 1. The records on which these analyses are based have been deposited at the East African Fisheries Organization, Jinja ; the punch-cards are at present stored in the Geofysisk Institut, Bergen, Norway, where the mechanical work was carried out, and will later be deposited at the British Museum (Natural History), London.

The way in which food items are grouped into categories (food-types) obviously influences the interpretation of the results. In making the groupings an attempt has been made to preserve taxonomic and ecological validity, while at the same time providing a system which extracts the greatest amount of information from variable material. A list of the food-types selected for analysis is given below, together with such biological notes as are necessary for an appreciation of their significance as fish-food. It must be emphasized that this is not a fauna list, but an annotated index of those items found most frequently in the stomachs of fishes. Unless specifically stated, species of insects were not distinguished ; the taxonomic revisions which would have made this practicable for a few groups became available only towards the end of this work.

In Table 1 the individual food-types are listed in alphabetical order under their abbreviated titles, as used throughout the main section of this paper. In Table 1 the code number (corresponding to the column on the punch-card) for each food-type is given so that details can be found quickly in the annotated list which follows. The abbreviated names are reference titles only, and are not necessarily comprehensive. Thus ' chironomid adults ' comprises adults of Chironomidae and/or Chaoboridae, as is made clear in the main list.

LIST OF FOOD-TYPES

The heading number refers to the number of the column on the punch-card (see Table 1).

19. Arthropoda. Includes all indeterminate arthropod remains, but not recognizable Insecta or Crustacea. Comprises almost entirely small spiders living on the water surface usually in or near grass swamp.

20. Insecta. Comprehensive : includes aquatic and terrestrial forms.

21. Chironomidae larvae. Most larvae eaten, especially by Mormyridae, appear to be mud-dwelling forms. Macdonald (1956) found the genera *Tanypus*, *Procladius* and *Chironomus* to be the most common in the mud of Ekunu Bay, a site where many of the present samples were obtained. He also demonstrated a lunar periodicity in their life-cycles which affects the feeding behaviour of *Mormyrus kannume* and perhaps related species also.

22. Chironomidae larvae, alive.

23. Chironomidae and/or Chaoboridae adults. Material was very often associated with pupal exuviae, indicating that it had been taken during an emergence. Apart from the three chironomid species and two

chaoborids listed by Macdonald (1956), at least three other chironomids and one chaoborid are known to show a lunar periodicity of emergence in Lake Victoria (Corbet, 1958 b and unpublished ; Tjønneland, 1958 a & b), and this must necessarily affect the habits of surface-feeding fishes. Taxonomic reviews of the Chironomidae (Freeman, 1955, 1956, 1957, 1958) and Chaoboridae (Verbeke, 1958) are available.

24. Chironomidae and/or Chaoboridae pupal breathing organs. These minute structures become detached from floating pupal exuviae after emergence and may become concentrated in such numbers as to resemble foam on the surface. They form a significant component of beach deposits in some places. Their presence in fish stomachs containing no pupae indicates surface-feeding habits. If these form the sole contents of a stomach it is recorded as being empty.
25. Chaoboridae larvae. Of the three species in Lake Victoria, only the larva of *Chaoborus anomalus* Edwards has been described (Verbeke, 1957 c). In his study of *Mormyrus kannume*, Macdonald (1956) recognized larvae of this and another species, and found that they are planktonic in the first two instars, during the first two weeks of larval life, but that in the remaining six weeks they spend the day in the mud and the night feeding in the plankton.
26. Chaoboridae larvae, alive.
27. Larvae of *Povilla adusta* Navas (Ephemeroptera, Polymitarcidae). Larvae of this burrowing mayfly, which attain a length of 25 mm., have been figured by Demoulin (1956) and Corbet (1957 b). Larvae line their burrows with a silk-like substance, and remain in them by day but swim actively after dark (Hartland-Rowe, 1958). Thus the association in a stomach of silken case and larva can indicate that the fish was extracting larvae from their burrows and not taking them freely in the water. In Lake Victoria a generation is usually completed in four or five lunar months ; thus larvae of a wide size-range are always available for the many species of fishes which prey on them (Corbet, 1957 b).
28. Adults of *P. adusta*. In this food-type are included sub-imagines, subimaginal exuviae and eggs which have already been laid. In Lake Victoria, emergence occurs shortly before sunset on a few days after full moon, the adults living for little more than an hour (Hartland-Rowe, 1955). Thus the time of feeding of the many fishes which contain adults can be specified. Eggs which have already been laid can be distinguished from those in the abdomen of full-grown larvae because they are surrounded by a swollen gelatinous matrix.
29. Ephemeroptera : burrowing larvae. In Lake Victoria these include *Eatonica schoutedeni* (Navas) (larva : Crass, 1947) and *Ephemera aequatorialis* Kimmins (Ephemeridae) ; and in rivers *Ephoron savignyi* Pictet (Polymitarcidae) (larva : Crass, 1947). *P. adusta* is not included.
30. Larvae of *Tricorythus tinctus* Kimmins (Ephemeroptera, Tricorythidae). Larvae (Corbet, 1960 b) cling to the surfaces of stones in swiftly-flowing water, where they provide food for many fishes.

31. Ephemeroptera : free-living larvae. This food-type includes all non-burrowing larvae except *T. tinctus* and *Afronurus ugandanus* Kimmins (Heptageniidae) (larva : Corbet, 1960 b) ; these consist mainly of Baetidae, Caenidae and Leptophlebiidae, which are common amongst plants and stones in the littoral zone.

32. Ephemeroptera : adults. All species except *P. adusta* (see Kimmins, 1956 a). Certain mayflies (e.g. *T. tinctus*, *Centroptilum notabile* Kimmins, and small species of *Caenis*) exhibit mass emergence at sporadic intervals, often at sunset, when they may be eaten in large numbers by fishes.

33. Ostracoda (Crustacea). No distinction was made between creeping and free-swimming forms.

34. Anisoptera larvae (Odonata). These are the largest aquatic insects to be eaten regularly by fishes, and they occupy a wide variety of niches in littoral and sub-littoral regions. Members of the Libellulidae achieve greatest importance amongst stands of plants (e.g. *Vallisneria*, *Najas*, *Potamogeton*) in the shallows, whereas the species which sprawl or burrow belong mainly to the Gomphidae (larvae : Corbet, 1956, 1957 a).

35. Zygoptera larvae (Odonata). Except for a few species which live under stones in rivers and exposed shores (e.g. *Metacnemis valida* Selys (larva : Corbet, 1956)), and the occurrence of which is always specifically mentioned, the species in this group belong almost entirely to the genus *Pseudagrion*, and live amongst aquatic plants in sheltered shallows.

36. Larvae of *Ictinogomphus ferox* Rambur (Odonata, Gomphidae). The larva (Corbet, 1956) rests on sandy or muddy bottoms and does not burrow. It may attain a length of 31 mm. when full-grown. During emergence, this species is heavily preyed upon by young crocodiles (Corbet, 1959).

37. Larvae of *Phyllomacromia* species (Odonata, Corduliidae). Only two species, *P. picta* (Selys) and *P. reginae* (Le Roi), are known from Lake Victoria. Their larvae (Corbet, 1957 a) are about 21 and 25 mm. long, respectively, and sprawl over sand in exposed situations.

38. Larvae of *Trithemis* species (Odonata, Libellulidae). Larvae are very common amongst sheltered stands of vegetation where they resemble the Palaearctic *Sympetrum* in facies.

39. Larvae of *Trithemis annulata* (Beauv.). This species is common and widespread in Lake Victoria. The larva is about 15 mm. long.

40. Larvae of *Brachythemis* species (Odonata, Libellulidae). This food-type includes the larvae (13–19 mm. long) of three species which resemble each other closely in morphology and habit (Corbet, 1957 a). They are *B. lacustris* Kirby, *B. leucosticta* (Burm.) and *Zyxomma flavicans* (Martin). All rest on sand or mud, but do not burrow.

41. Pupae of Chironomidae and/or Chaoboridae. If represented in large numbers in a stomach with few or no larvae, these are considered to indicate a surface-feeding habit.

42. Larvae and/or adults of Corixidae (Hemiptera). These comprise species of *Micronecta*, including *M. dimidiata* Poisson and *M. druryana* Hutch. This family is not well-represented in Lake Victoria.

43. Larvae of Trichoptera. Although adults, mainly Leptoceridae (see Kimmins, 1956 b) and Hydropsychidae, are very numerous in the lake, larvae have proved difficult to find, and so far only eight have been described (Hickin, 1955, 1956 ; Marlier, 1956 ; Corbet, 1958 c).

44. Larvae of *Phanostoma senegalense* Brauer (Trichoptera, Hydropsychidae). Larvae (Hickin, 1955) are about 13 mm. long, and dwell in cylindrical silken cases on rocks in rivers or on exposed shores of the lake.

45. Larvae of *Ecnomus* species (Trichoptera, Psychomyidae). There are several very abundant species (see Kimmins, 1957). Larvae (Corbet, 1958 c) are more important as fish-food than any other caddisfly in the lake. They are free-living, apparently on algae-covered rocks on wave-washed shores (Verbeke, in Jacquemart, 1957).

46. Larvae of Hydroptilidae (Trichoptera). These include species of *Orthotrichia*. Larvae (Corbet, 1958 c) dwell in small seed-like cases, about 3 mm. long, attached to leaves of aquatic plants, or to the surfaces of stones in rivers or on exposed shores.

47. Pupae and/or adults of Trichoptera. These are usually eaten at the surface during emergence, probably near the time of sunset (see Corbet & Tjønneland, 1955).

48. Hydracarina. Several species are abundant amongst sheltered marginal vegetation.

49. Hydracarina, alive.

50. *Caridina* (Crustacea, Decapoda, Atyidae). It is probable that all the prawns encountered belonged to the single variable species, *Caridina nilotica* (Roux) (Gordon, 1930).

51. *Potamon* (Crustacea, Decapoda, Potamonidae). All crabs found in fish-stomachs were referable to *P. niloticus* (Milne-Edwards). This species is very common amongst rocks in rivers and on exposed shores, and individuals with a carapace-width of 70 mm. are sometimes found.

52. Parasitic Nematoda. If these form the sole contents, a stomach is recorded as being empty.

53. Parasitic Nematoda, alive.

54. Larvae and/or adults of aquatic Coleoptera.

55. Terrestrial insects. A comprehensive category, including food-types 56 and 57.

56. Isoptera, adults. These include at least two species of *Macrotermes*, *M. bellicosus* (Smenth.) and *M. natalensis* (Hav.), which are said to fly between midnight and dawn (Harris, personal communication). These are taken at the surface.

57. Hymenoptera, adults. These consist mainly of ants, particularly Camponotinae, which are taken at the surface.

58. Mollusca. A taxonomic review of this group is available (Mandahl-Barth, 1954), and the nomenclature given therein is followed in this paper.
59. Gastropoda.
60. *Melanoides tuberculata dautzenbergi* Pilsbry & Bequaert (Gastropoda, Thiaridae). A very common and almost ubiquitous mollusc in Lake Victoria and the Victoria Nile.
61. *Bellamya* species (Gastropoda, Viviparidae). In Lake Victoria these are all referable to subspecies of two variable species, *B. unicolor* Olivier and *B. jucunda* Smith.
62. Pelecypoda.
63. Pelecypoda, small species (Corbiculidae, Sphaeriidae). Bivalves 2 to 12 mm. long of the genera *Corbicula*, *Sphaerium*, *Pisidium* and *Byssanodonta*.
64. Pelecypoda, large species (Unionidae, Mutelidae). Bivalves 20 to 135 mm. long of the genera *Caelatura*, *Mutela*, *Aspatharia* and *Etheria*.
65. Pisces. For the mormyrids, *Gnathonemus longibarbis* and *G. victoriae* this category includes fish eggs. In *Marcusenius grahami* only, it denotes larvae and/or adults of Tipulidae (Diptera).
66. Cichlidae. This includes species of *Haplochromis* and related genera, and *Tilapia*.
67. *Haplochromis* and related genera, which comprise *Astatoreochromis*, *Hoplotilapia*, *Macropleurodus*, *Paralabidochromis* and *Platytaeniodus*.
68. *Haplochromis* and related genera normally found over a hard bottom.
69. *Haplochromis* and related genera normally found over a soft bottom.
70. *Haplochromis* and related genera found over both hard and soft bottoms.
71. *Tilapia* species. In the present study, this category probably included only *T. variabilis* and *T. esculenta*. The Lake Albert species, *T. zilli* (Gervais), was introduced while the work was in progress, but it is extremely unlikely that it could have reached the localities studied in time to affect the results. In *Synodontis victoriae* only, category 71 denotes parasitic Cestoda.
72. Pisces, other than Cichlidae. Most non-cichlid species in the lake belong to the Mormyridae, or to the Siluroidea (Bagridae, Clariidae, Schilbeidae and Mochocidae) ; but the only species commonly eaten by other fishes is a cyprinid, given separate status as the next food-type.
73. *Engraulicypris argenteus* (Cyprinidae). A small fish about 70 mm. long, occurring in shoals near the surface of the lake, and in the Victoria Nile. In *Synodontis victoriae* only, category 73 denotes unidentified eggs, possibly of Gastropoda.
74. Plant material (Phanerogamae), dead. In the cases of known carnivores, such as *Clariallabes petricola* or *Clarias mossambicus*, a stomach containing *only* dead plant material would be recorded as empty. In *Synodontis victoriae* only, category 74 may include tests of colonial Bryozoa which were confused with lithophilic roots at the beginning of the study.

75. Plant material (Phanerogamae), living—having obviously been bitten off a plant.
76. Plant material (Phanerogamae), living—but not showing obvious signs of having been bitten off a plant.
77. Masticated seeds of water lilies (*Nymphaea* sp.). In *Protopterus aethiopicus* only, category 77 denotes mosquito larvae (Culicinae).
78. "Flower-buds". Unidentified objects resembling small partly-opened flower-buds about 3 mm in diameter. These were almost certainly split eye-lenses of fishes.
79. Sand grains. If this or the following category provides the only contents, a stomach is recorded as being empty. In bottom feeders the presence of sand grains can be used to confirm the provenance of items in the stomach.
80. Pebbles and small stones.

In the following section food-types are given in abbreviated form as listed in Table 1, to which reference can first be made if details of any particular food-types are required from the above list. Any exceptions to this list are described under the species concerned.

THE FOOD OF THE FISHES

LEPIDOSIRENIDAE

PROTOPTERUS AETHIOPICUS Heckel

In Lake Victoria the lungfish, *Protopterus*, breeds in marginal swamps of semi-aquatic grass and papyrus. The young remain in the nest for some seven or eight weeks, until they are about 30 to 40 mm. long (see Greenwood, 1958). It is not known how much longer the young fishes remain in the swamp before they enter the lake proper. It is clear, however, that the food of lungfishes obtained from the two habitats should be assessed separately.

In the present study food analyses were based on the contents of the whole spiral valve. Fishes examined were derived as shown in Table 2 ; and 90·1 per cent of them contained food.

TABLE 2

Derivation of *Protopterus aethiopicus*.

	Lake Victoria				Victoria Nile	Totals
	Marginal Swamp	Lake				
		HARD	MIXED	SOFT		
Numbers examined	64	13	152	92	12	335
Numbers containing food	52	13	145	82	10	302
Size-ranges (cm.)	3–32	34–127	43–118	49–130	16–133	3–133

The food of fishes from samples large enough to merit analysis is given in Tables 3 and 4.

TABLE 3

Protopterus aethiopicus : percentage occurrence in swamp and lake.

Food	Marginal Swamp	Lake	
		MIXED	SOFT
Arthropods	14	—	—
Insects	83	20·0	10
Chironomid larvae	17	17·2	2
Culicine larvae	19	—	—
Tricorythus larvae	—	—	1
Anisoptera larvae	4	2·1	7
Ictinogomphus larvae	—	1·4	5
Zygoptera larvae	2	—	—
Trichoptera larvae	2	—	—
Coleoptera	46	—	1
Terrestrial insects	12	0·7	—
Ostracoda	—	0·7	—
Caridina	—	1·4	—
Potamon	—	—	2
Molluscs	8	95·9	94
Gastropoda	8	91·7	92
Melanoides	—	90·3	49
Bellamya	2	38·6	88
Pelecypoda	2	83·4	70
small species	2	77·9	45
large species	—	15·9	32
Fishes	4	30·3	16
Cichlidae	2	22·8	9
Haplochromis	2	16·6	9
Tilapia	—	0·7	—
Non-cichlids	—	0·7	—
Plants, dead	22	2·0	7

TABLE 4

Protopterus aethiopicus : percentage main contents in swamp and lake.

Food	Marginal swamp	Lake	
		MIXED	SOFT
Arthropods	8	—	—
Insects	39	1·4	1
Anisoptera larvae	6	1·4	1
Zygoptera larvae	2	—	—
Coleoptera	8	—	—
Molluscs	—	71·7	83
Gastropoda	—	26·2	56
Melanoides	—	24·8	4
Bellamya	—	—	49
Pelecypoda	—	11·7	7
small species	—	9·0	4
large species	—	2·1	4
Fishes	—	9·0	4
Cichlidae	—	6·2	4
Haplochromis	—	4·8	4
Tilapia	—	0·7	—

Marginal swamp

The food of small fishes in marginal swamp consists almost entirely of insects, amongst which the most important by volume are larvae and adults of aquatic Coleoptera, and larvae of Odonata. Beetles identified from guts were : *Canthydrus* and *Hydrocanthus* (Dytiscidae–Noterinae) ; Helodidae–Cyponinae ; *Eretes sticticus* L. (Dytiscidae) ; and *Spercheus cerisyi* Guér. (Hydrophilidae). The Odonata, which were mainly Anisoptera, included *Sympetrum navasi* Lacroix and *Ceriagrion*, both of which are known to be swamp-dwellers. The mosquito larvae eaten were all culicines. Other food was various, and comprised spiders, terrestrial bugs and beetles, aquatic bugs (*Laccotrephes*), land snails, swamp worms (*Alma*), and small fishes. Of the *Protopterus* examined from swamps, only those over 20 cm. long had eaten Odonata larvae.

Lake

From his examination of eleven fishes, Graham (1929) concluded that lungfishes fed largely on molluscs. My records confirm this : amongst fishes 43–130 cm. long, about 95 per cent contained molluscs, 92 per cent gastropods and 70–83 per cent pelecypods. Of the two groups, gastropods are by volume far the more important food, especially over a soft bottom, where they may

TABLE 5

Protopterus aethiopicus : percentage occurrence of mollusc genera.

Gastropoda	
Melanoides	72·5
Bellamya	57·5
Biomphalaria	2·5
Gabbia	1·6
Pila	1·2
Bulinus	0·8
Lymnaea	0·4
Pelecypoda—small	
Sphaerium	63·8
Corbicula	4·0
Pelecypoda—large	
Caelatura	22·4
Etheria	0·8
Mutela	0·4

provide the main contents in 56 per cent of fishes. *Melanoides tuberculata* (noted also by Graham) and species of *Bellamya* are the gastropods eaten most often, the former more where the bottom is mixed, and the latter more where it is soft. The occurrence of different genera of molluscs in the combined lake sample of *Protopterus* is recorded in Table 5, from which it is clear that species of *Sphaerium* and *Caelatura* (mainly *C. cridlandi*) are the most important pelecypods. Species so far recorded from *Protopterus* are listed on page 17, the nomenclature being that of Mandahl-Barth (1954).

Bellamya unicolor unicolor
Bellamya unicolor elatior
Bellamya unicolor trochlearis
Bellamya unicolor costulata
Bellamya unicolor ugandae
Bellamya unicolor dagusiae
Bellamya unicolor constricta
Bellamya jucunda jucunda
Bellamya jucunda altior
Bellamya jucunda kisumiensis
Pila ovata
Gabbia humerosa humerosa
Melanoides tuberculata dautzenbergi
Lymnaea
Biomphalaria choanomphala
Bulinus trigonus strigosus
Caelatura hauttecoeri hauttecoeri
Caelatura hauttecoeri grandidieri
Caelatura hauttecoeri emini
Caelatura hauttecoeri ruellani
Caelatura cridlandi
Caelatura monceti
Mutela bourguignati
Etheria elliptica
Corbicula africana cunningtoni
Sphaerium victoriae victoriae
Sphaerium stuhlmanni stuhlmanni
Sphaerium stuhlmanni regularis
Sphaerium nyanzae nyanzae

Records suggest that lungfishes of 70 cm. and over may eat more large pelecypods than those below this size. If this is so, it may be a simple expression of the size of the mouth of *Protopterus* and the strength of its jaws, which are used to crush the shells of the molluscs it eats. It is possible that the largest pelecypods, such as *Mutela*, may become increasingly important to very large *Protopterus*, which are not well represented in my sample. It may be noted that the largest fish examined (*ca.* 180 cm.) had fed almost entirely on *Mutela*.

Fish remains can provide the main contents in 4–9 per cent of individuals, but as food they do not achieve more than one-eighth the importance by volume of molluscs. Almost all the fishes eaten are cichlids, and almost all of these are *Haplochromis*. *Tilapia* or non-cichlids were found in only 1·7 per cent of fish-eating *Protopterus* and in only 0·4 per cent of all those containing food. The single record of *Tilapia* was a *T. esculenta* 28 cm. long in a lungfish 118 cm. long weighing 24½ lb. The non-cichlids eaten included a small *Synodontis* (*ca.* 6 cm.), *Bagrus*?, *Barbus*?, and a small cyprinid.

It has long been alleged that *Protopterus* bite and damage other fishes already netted (see Greenwood, 1955 a). The present records support this claim in so far as the fish remains were almost invariably represented by small fragments derived from a limited part of the body. This situation differs markedly from that encountered in a piscivore such as *Bagrus docmac*, in which fishes in the stomach are entire, or, if fragmented, then usually represented by the whole body.

A few specimens in the lake had fed on insects, these being mainly chironomid and Anisoptera larvae. The latter included *Ictinogomphus ferox* and *Brachythemis leucosticta*, both of which rest on the surface of sediment. An exceptional fish containing adult termites had perhaps taken them while surfacing to breathe.

It is interesting to note that lungfishes can be caught on a line baited with meal paste (Graham, 1929), although this does not necessarily imply any counterpart in their preferred food. Fishermen at the mouth of the Kagera

River bait long lines with appendages of crabs, and claim to catch *Protopterus* on them, but it is clear from the present records that in Lake Victoria neither *Potamon* nor *Caridina* is eaten other than occasionally : in the lake both items occurred in only 0·8 per cent of fishes—from mixed and soft bottoms respectively. Crabs may be a more important food of this species in Lake Tanganyika (Poll, 1953).

Occasional records exist of *P. aethiopicus* taking birds from the surface in Lake Victoria (Pitman, 1957).

Victoria Nile

Seven specimens (16–33 cm.) had fed mainly on lithophilic insects (*Tricorythus*, Hydropsychidae, *Ecnomus*) and on small fishes. Two specimens (89, 133 cm.) had eaten mostly *Caelatura* (including *C. hautticoeri*), but also *Melanoides*, *Bellamya*, *Biomphalaria*, *Bulinus* and *Lymnaea*. The smaller fish had also eaten a final instar larva of *Ictinogomphus ferox*.

Conclusions

Whether living on a river-bed or in a lake-side swamp, young *Protopterus* less than 35 cm. long feed almost wholly on insects. Individuals above this size, in a river or lake, are specialized mollusc-eaters, using their powerful jaws to crush the shells into small fragments. They eat a wide variety of species, but gastropods (especially *Melanoides* and *Bellamya*) always provide the main bulk of their food. Fishes, consisting almost entirely of *Haplochromis*, are of relatively minor importance as food, although eaten regularly in small quantities. Almost all fish remains consist of small fragments, probably torn from fishes already caught in nets. It cannot be concluded, either from this study or from previous work (Graham, 1929), that *Protopterus* is of any importance as a predator of *Tilapia* in Lake Victoria. Indeed, from an ecological viewpoint, it is possibly incorrect to regard *Protopterus* even as a predator of *Haplochromis*, since it is likely that it feeds very largely on those fishes which have been caught already by man. Since it became known that *Protopterus* was a preferred food of larger crocodiles in Lake Victoria (Cott, 1954), it has been suggested that continued exploitation of crocodiles might relieve the pressure on " predatory " species such as *Protopterus* and thereby endanger stocks of cichlids. The evidence given here, however, indicates that *Protopterus* is a damager, rather than a predator, of fishes, and that the only predictable danger of its increase lies in that direction. This view is supported by records of some *Protopterus* obtained from the Nantongo Estate Dam, Uganda, in which there were many *Tilapia esculenta*, but very few molluscs. The *Protopterus*, which averaged 4·5 lb. (range *ca.* 1–26 lb.), had been feeding almost entirely on small frogs, whereas the *Tilapia* population " appeared under-fished " (U.G.G.F.D., 1953, p. 128).

Crocodiles and man are apparently the main predators of *Protopterus* in the lake. Graham (1929) found one 10 cm. long in the stomach of an otter (presumably *Lutra* (*Hydrictis*) *maculicollis* Lichtenstein) in Lake Victoria. The only record known to me of predation occurring in the swamp habitat is that of a spider catching a larval *Protopterus* as it surfaced at the margin of a nest (D. J. Garrod, personal communication).

MORMYRIDAE

MORMYRUS MACROCEPHALUS Worthington

Although known previously from Lake Kyoga and the Victoria Nile, this species was not taken in Lake Victoria until early in 1956, when a single adult was caught at Bugungu, near Jinja. Since then other specimens have been taken in the lake, nine of which have been examined for stomach contents. Entrance to the lake is thought to have been achieved *via* turbine housings in the Owen Falls Dam.

TABLE 6

Mormyrus macrocephalus : occurrence and (main contents) in river and lake.

Food	Victoria Nile	Lake
Insects	22 (8)	8 (2)
Chironomid larvae	5 (1)	4
Chaoborid larvae	2	–
Povilla larvae	15 (2)	5
Tricorythus larvae	5	–
Ephemeroptera : free-living larvae	9	2
Anisoptera larvae	10 (2)	5 (1)
Zygoptera larvae	4	1
Trichoptera larvae	5	–
Tipulid larvae	1	1 (1)
Caridina	1	7
Gastropoda	5	1
Fishes	4	6 (3)
Cichlidae	2	3 (2)
Haplochromis	1	3 (2)
Non-cichlids	—	2 (1)
Plants dead	10 (3)	5
Number of fishes containing food	22	9

Victoria Nile

Twenty-two fishes (7–49 cm.) were examined, all of which contained food. They were obtained from the Victoria Nile about 200 m. below the Owen Falls Dam, on occasions when lowering of the water level there made collecting possible. Some of the smaller fishes were obtained from the rocks of the river bed, but most came from a pool in a grass swamp connected to the main river.

Table 6 shows that the fishes had been feeding mainly on insects, but that these had been obtained from two different sources—river bed and swamp. It was the smaller fishes that had been feeding amongst stones : characteristic lithophilic forms such as the mayflies *Tricorythus* and *Euthraulus*, and the hydropsychid caddisflies *Cheumatopsyche copiosa* Kimmins and *C. falcifera* Ulmer were found only in fishes 8–11 cm. long. Larger fishes (20–49 cm.) had apparently been feeding mainly in the swamp, since, amongst other things, they contained much dead plant material, swamp-living Odonata

larvae (*Trithemis*, *Ceriagrion*) and a water-stick-insect (*Ranatra cf. parvipes* Sign.). In both size-groups of fishes *Povilla* larvae (often with their silken tubes) were common, a finding consistent with the knowledge that larvae can live in sheltered marginal vegetation (Hartland-Rowe, 1958) or in a swift current (Corbet, 1958 a). The Gastropoda eaten included small *Biomphalaria*, *Gabbia* and *Gyraulus*. The Anisoptera larvae were mostly Libellulidae (mainly final instar), but included a gomphid (*Ictinogomphus*?). The Zygoptera included species of *Ceriagrion* and *Pseudagrion*. Occasional food comprised an aquatic bug, *Sphaerodema* sp. (known to live amongst stones), Ostracoda, and a terrestrial hymenopteran. Fishes and *Caridina* did not appear to be important foods, but it is interesting to note that in each of two specimens (32 and 42 cm.), caught on different occasions, the stomach contained a large ball of tin foil. It is probable that the foil had been taken in mistake for a fish. The smallest individual containing fish remains was 27 cm. long, and so it is likely that fishes are eaten more by larger individuals.

Lake Victoria

Nine fishes (31–57 cm.) were examined, and all contained food. They came from two soft bottom habitats, each with a marginal swamp close at hand. The sample, though small, is sufficient to indicate that food was obtained from marginal vegetation as well as from the bottom. It appears that small fishes form an important food. Although these are mainly *Haplochromis*, one specimen (46 cm.) had eaten thirteen non-cichlids, including at least seven *Aplocheilichthys pumilus*. Another (51 cm.) contained a mormyrid, probably *Marcusenius nigricans*, about 5 cm. long. *Caridina* is more important here, and Odonata larvae (again mainly Libellulidae) include *Trithemis*, *Brachythemis leucosticta* (the mud-dwelling form—see Corbet, 1957 a), *Phyllomacromia picta* and *Ictinogomphus ferox* (the latter two being sprawlers and not burrowers). The gastropod was *Bellamya*. Other items included Ostracoda, Hydracarina and Hirudinea. Thus, in the lake *M. macrocephalus* was feeding on fishes, the largest insects, and *Caridina*.

Conclusions

Worthington (1929) obtained records from twenty-two stomachs, from Lake Kyoga and the Victoria Nile, and found insect larvae in twelve, fishes in six, and prawns in two. My sample of thirty stomachs indicates that in the river, when less than 11 cm. long, *M. macrocephalus* feeds amongst stones on small lithophilic insects, whereas larger individuals in the same site feed more amongst marginal vegetation, a habit also shown by fishes of comparable size in Lake Victoria.

When small (probably less than 20 cm.) and feeding amongst stones, *M. macrocephalus* is predominantly insectivorous, but after this it soon concentrates on larger organisms such as *Caridina*, small fishes and the largest insects, namely *Povilla* and Odonata larvae. Fishes over 20 cm. long are probably rarely predominantly insectivorous except where large insects are unusually abundant. It appears that they are generalized feeders able to utilize most types of animal prey which is of an appropriate size. In some

places larger individuals probably feed extensively on small fishes in marginal vegetation. The presence of tin foil in two stomachs suggests that they hunt them mainly by sight, although there is the alternative possibility that the tin foil may have been perceived by its effect on the electric field (see Lissmann, 1958).

Nothing is known of the breeding habits of this species, but the food and site of capture of the smallest fishes suggests that it may perhaps spawn in rocky riverine habitats. If this is so, adult fishes should be encountered moving into affluent rivers of Lake Kyoga at the time of breeding.

MORMYRUS KANNUME Forskål

Mormyrus kannume is one of the commonest non-cichlids in Lake Victoria and is found in a wide variety of habitats of moderate depth. Nothing definite is known of its breeding habits, although in 1956 several small *M. kannume* down to 3 cm. in length were found feeding amongst rocks on the bed of the Victoria Nile. This was the first occasion on which fishes smaller than about 15 cm. had been caught, except in the stomachs of predators. If small *Mormyrus* do inhabit exposed rocky shores in Lake Victoria, it is clear that evidence of this would be difficult to obtain by conventional means. Therefore it may be assumed for the moment that the description of the feeding habits of small fishes from the Victoria Nile applies also to those in the lake, for which records are at present lacking.

TABLE 7

Derivation of *Mormyrus kannume*.

	Lake Victoria			Victoria Nile	Totals
	HARD	MIXED	SOFT		
Numbers examined	1294	1159	340	39	2832
Numbers containing food	1170	1133	312	33	2648
Size-ranges (cm.)	15–52	16–62	17–49	3–20	3–62

Victoria Nile

The feeding habits of *M. kannume* in the Victoria Nile, and the ways in which these were affected by DDT have already been described (Corbet, 1958 a). Under normal conditions, small fishes living amongst the rocks of the river bed fed almost entirely on lithophilic insects, amongst which larvae of *Tricorythus*, *Phanostoma*, *Cheumatopsyche copiosa* and Hydroptilidae were the most important, whereas other food included larvae of *Povilla*, *Cheumatopsyche falcifera*, *Pseudoleptocerus schoutedeni* Navas, Baetidae, Caenidae, Ostracoda, Hydracarina, chironomid larvae and aquatic Coleoptera—the latter probably being obtained from a nearby swamp. It is clear, however, that most of the food was being taken from the surfaces of stones.

Under the abnormal conditions imposed by the DDT treatment, which temporarily removed the lithophilic insects, the few fishes which contained

food had been eating chironomid and tipulid larvae, Hydracarina, Conchostraca, and aquatic beetles. It appeared that relatively more feeding was occurring in sheltered marginal vegetation. It is interesting to note that one fish (11 cm.) had eaten a pupa of *Simulium alcocki* Pomeroy. Possibly, in habitats where *Simulium* are abundant, small *Mormyrus* may feed heavily on their larvae. In this connection it should be noted that, although known to be common on the river bed, *Afronurus* larvae were not found in *Mormyrus* stomachs. Were *Mormyrus* to reject them for some reason, this might represent an ecological advantage to *Simulium* of the phoretic association existing between itself and *Afronurus*.

Lake Victoria

From previous studies of *M. kannume* it has been concluded that its food in the lake, particularly over mud, consists very largely of chironomid and chaoborid larvae (Graham, 1929 ; E.A.F.R.O., 1948). Over sand and rock its food is more varied and includes greater numbers of caddisfly and mayfly larvae (particularly *Povilla*) and *Caridina* (E.A.F.R.O., 1951, 1952). Most feeding activity apparently occurs at night (see Macdonald, 1953).

Macdonald (1956) who made a special study of the chironomid larvae eaten by *Mormyrus*, recorded that over a muddy bottom (Ekunu Bay), the food was composed mainly of three species, *Tanypus guttatipennis* Goetg., *Procladius brevipetiolatus* Goetg. and a *Chironomus* species of the *plumosus* type, whereas there were also small numbers of *Clinotanypus*, *Tanytarsus* and other genera. Macdonald demonstrated that the main food species in Ekunu Bay, namely the three chironomids and two chaoborids, showed a lunar periodicity of development and emergence, which could be discerned by its effect on the food of the fishes. Over a rocky bottom (near Jinja), where *Povilla* larvae form an important food, a similar situation has been recorded (Corbet, 1957 b). It is therefore evident that any assessment of *M. kannume* food must make allowance for habitat, size of fish and time of lunar month.

Habitat

The samples from which Tables 8 and 9 were derived (see Table 7) were collected without conscious bias as to size or lunar phase, and I therefore consider that they provide a fair measure of food differences due to habitat alone.

In Table 9 no values have been given for the inclusive item ' insects ', since these would be virtually 100 per cent for all habitats (see Table 8). In fact, in only one fish was the main contents not insect remains : this was an exceptional individual which had been feeding on small fishes.

These results show that *M. kannume* is almost exclusively insectivorous and that chironomid larvae are by far its most important food. These occur in 90–100 per cent of fishes over 15 cm. long, irrespective of their feeding grounds, and provide the main contents in 40–90 per cent.

Though still providing the main food there, chironomid larvae are of least relative importance over hard-bottom feeding grounds, where *Mormyrus* has a more varied diet and feeds to a greater extent than elsewhere on larvae of

TABLE 8

Mormyrus kannume : percentage occurrence in Lake Victoria.

Food	HARD	MIXED	SOFT
Insects	99·9	100·0	100·0
Chironomid larvae	90·3	99·3	95·8
Chaoborid larvae	34·6	77·1	54·8
Povilla larvae	40·3	6·2	16·3
Ephemeroptera : burrowing larvae	0·2	—	0·6
Ephemeroptera : free-living larvae	44·1	7·6	20·0
Tricorythus larvae	2·6	0·3	—
Anisoptera larvae	5·1	3·8	6·1
Zygoptera larvae	0·5	0·4	1·6
Trichoptera larvae	48·5	5·6	19·2
Ecnomus	38·1	4·9	15·1
Phanostoma	5·5	—	1·3
Hydroptilidae	4·1	0·2	1·3
Corixidae	3·4	4·3	1·3
Coleoptera	—	0·1	1·0
Hydracarina	7·9	0·3	1·9
Ostracoda	31·3	15·5	14·4
Caridina	7·5	7·1	2·9
Potamon	0·1	—	0·3
Molluscs	5·0	0·3	3·8
Fishes	1·0	0·2	0·3
Cichlidae	0·4	0·1	0·3
Non-cichlids	0·3	0·1	—
Surface forms			
Chironomid adults	0·1	0·1	—
Povilla adults	0·6	0·2	—
Ephemeroptera adults	0·3	—	—
Terrestrial Hymenoptera	0·2	—	—
Sand grains	17·7	1·2	5·9
Pebbles	0·5	0·8	1·5

TABLE 9

Mormyrus kannume : percentage main contents.

Food	HARD	MIXED	SOFT
Insects			
Chironomid larvae	41·8	88·4	74·0
Chaoborid larvae	2·8	0·1	1·8
Povilla larvae	9·8	1·3	4·7
Ephemeroptera : free-living larvae	3·9	0·3	1·4
Tricorythus larvae	0·1	—	—
Anisoptera larvae	0·9	0·3	0·7
Trichoptera larvae	1·6	0·2	0·7
Ecnomus	1·1	0·2	0·7
Phanostoma	0·3	—	—
Caridina	0·4	0·3	—
Fishes	0·1	—	—

Povilla, other Ephemeroptera, and Trichoptera. But none of the latter achieves more than one quarter the importance of chironomid larvae, even though at certain times and in certain habitats these three items may each occur in 40–50 per cent of stomachs.

The Odonata eaten by *M. kannume* are mainly Libellulidae. It is noteworthy that almost all are species which rest on the top of sediment. Only three fishes contained burrowing larvae, two of which (*Paragomphus*, *Crenigomphus*) live in sand, and one (*Orthetrum*) in mud.

Occasional food, not mentioned above, includes swamp worms (*Alma*), Plecoptera larvae (*Neoperla spio* (Newman)) (larva: Hynes, 1953), Conchostraca and small mollusc shells. The latter were of one pelecypod and seven gastropod genera, and their worn but unbroken condition indicated that they had been ingested accidentally with other bottom deposits. It is possible that some Ostracoda and fish eggs are eaten in the same manner.

Size

Occurrences of the twenty commonest food items were analyzed according to five size-groups of fish from four habitats—two hard and two mixed. Of the foods which show a change of incidence with size, the only ones mentioned here are those which provide the main contents, and are therefore likely to be of some importance in the diet. These comprise five items, the occurrence of which is shown in Figs. 2–11. The changes observed are statistically significant to the extent shown in Table 10. To produce the figures and table, values for both hard bottom habitats, and both mixed bottom habitats, respectively, have been combined, since the trends were the same in each.

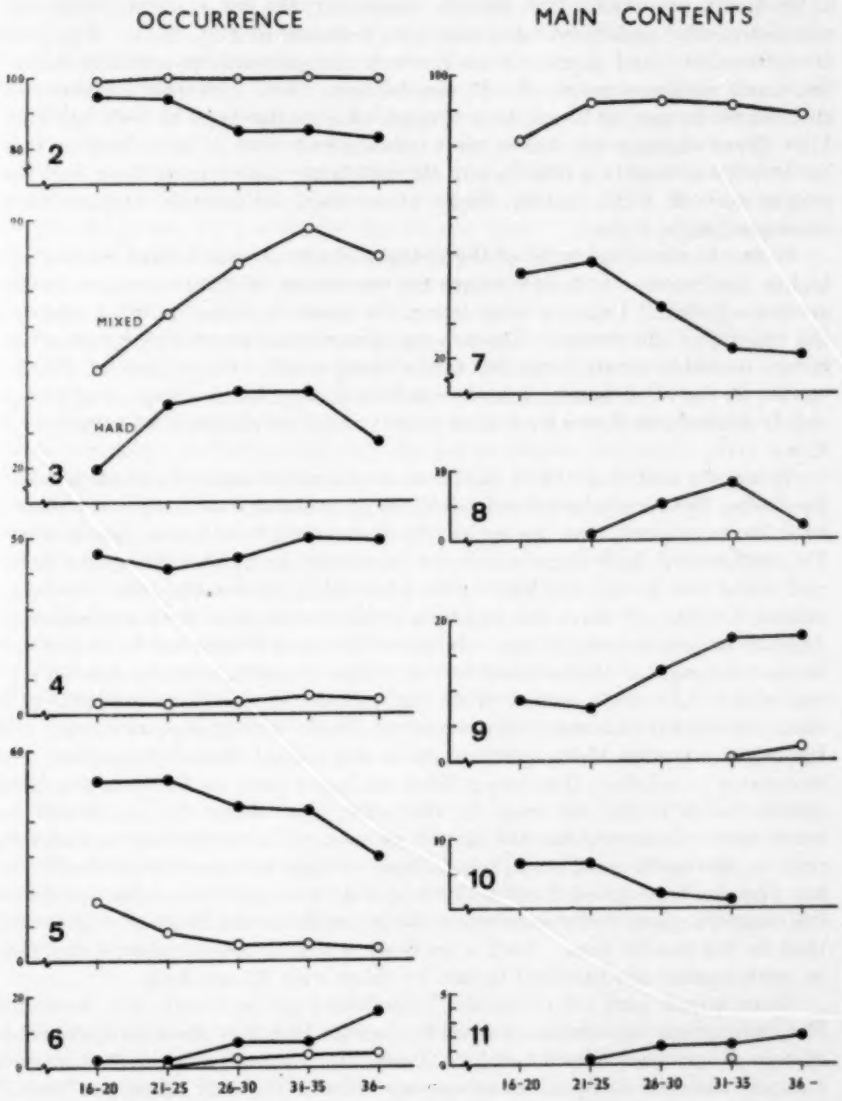
An important feature of the graphs is that the changes shown by occurrence values in the two types of habitat follow the same patterns as those shown by main contents values for the corresponding items. As these two statistics are

TABLE 10

M. kannume: statistical significance of changes of food with size of fish. All X^2 values are for 4 degrees of freedom.

Food	HARD BOTTOM				MIXED BOTTOM			
	Occurrence		Main contents		Occurrence		Main contents	
	X^2	P	X^2	P	X^2	P	X^2	P
Chironomid larvae	25·0364	.	38·1563	.	4·6593	>·30	7·6171	>·10
Chaoborid larvae	37·1669	.	31·3010	.	60·4117	.	2·3342	>·50
Povilla larvae	3·7570	>·30	14·4622	<·01	1·8086	>·75	9·1511	>·05
Ephemeroptera larvae	12·7519	<·02	16·1654	<·005	18·0431	<·005	—	
Anisoptera larvae	25·1355	.	5·5877	>·20	4·2631	>·50	2·3342	>·50

If no value for P is given, it is less than ·001, and the change of food with size is therefore highly significant.



Figs. 2–11.—*Mormyrus kannume*. Change of food with size in Lake Victoria, over a mixed bottom (empty circles) and over a hard bottom (full circles).
Figs. 2 and 7. Chironomid larvae ; Figs. 3 and 8. Chaoborid larvae ; Figs. 4 and 9. *Povilla* larvae ; Figs. 5 and 10. Ephemeroptera : free-living larvae; Figs. 6 and 11. Anisoptera larvae.
Abscissa : size-groups in cm.
Ordinate : percentage occurrence (Figs. 2–6) or main contents (Figs. 7–11).

almost independent of each other, such correspondence emphasizes the validity of the trends observed. It is for this reason that the few examples which are not statistically significant have also been included in Figs. 2–11. The data are informative, and in most cases the lack of significance is probably due to the small numbers involved. It can be seen that, with the exception of chironomid larvae, all items show changes of a similar type in both habitats. That these changes are much more pronounced over a hard bottom (see Table 10) is evidently a reflection of the diet being more varied there, and the proportions of fishes eating foods other than chironomid larvae being correspondingly higher.

It can be seen that most of the changes observed over a hard bottom are highly significant. Although values for occurrence of Ephemeroptera larvae are less significant than for other items, the trend for main contents confirms the validity of the change. The non-significant series recorded for Anisoptera larvae probably result from the totals being small. Occurrence of *Povilla* larvae, on the other hand, probably exhibits no significant change, despite the clearly defined one shown for main contents, since the numbers are consistently high.

It may be said that over a hard bottom the importance of chironomid and free-living Ephemeroptera larvae declines progressively with size. It should here be mentioned that many of the Ephemeroptera larvae (particularly *Tricorythus* and *Euthraulus* which are prominent in smaller fishes) are lithophilic, and that in the only habitat for which adequate records exist, two other lithophilic items, *Phanostoma* and hydroptilid larvae, also show a progressive decrease in occurrence with size. Initially this trend is balanced by an increase in the consumption of chaoborid larvae, which are eaten most by fishes 31–35 cm. long. This trend is also offset, throughout the size-range studied, by a small but regular increase in importance of *Povilla* and Anisoptera larvae. As the latter represent the largest insects in the normal diet of *Mormyrus*, it is reasonable to conclude that larger fishes eat larger prey, as, for example, Allen (1939) found to be the case in the pike, *Esox lucius* L. It should be remembered, however, that the largest Anisoptera do not become available as prey to *Mormyrus* until its mouth is large enough to ingest them whole. It has already been noted (Corbet, 1957 b) that amongst *Mormyrus* caught at the same time and in the same place the larger fishes eat larger *Povilla* larvae than do the smaller ones. Such a tendency would be consistent with the drop in consumption of chaoborid larvae by fishes over 35 cm. long.

Over mixed (and soft) bottoms, chironomid larvae remain the dominant food throughout the size-range studied, during which they show no appreciable change of incidence (Figs. 2 and 7 ; Table 10). It is significant that in such habitats these, and chaoborid larvae, are usually the only abundant benthic insects available. Changes in food with size over a mixed bottom are far less marked than over a hard bottom, but those recorded for two items must be mentioned. There is, once again, a highly significant decline in Ephemeroptera larvae, indicating that larger fishes feed progressively less in the hard-bottom parts of the habitats ; and chaoborid larvae, though eaten far less than over a hard bottom, show essentially the same pattern of size-dependent

incidence. The explanation of this well-defined change is not obvious. In the lower part of the size-range the regular increase in consumption of chaoborid larvae is doubtless a direct consequence of fishes feeding more in mud, but the consistent decline observed at the upper end of the range is less easily explained. That it could be due, over a mixed bottom, to a need for larger prey (see above) seems unlikely since firstly, there is no corresponding decline in chironomid larvae, which are much the same size, and secondly, very little other prey is eaten. In fact from this point of view it is surprising, because the life-history of *Chaoborus* is such (Macdonald, 1956) that the largest larvae and pupae are present for the longest time. There is perhaps a possibility that larger *Mormyrus* may have a slightly different diel feeding rhythm, and thus encounter fewer chaoborid larvae while they are in the mud during the day. The lack of significance of changes shown by *Povilla* and Anisoptera larvae could well be due to the very small numbers involved. Although the records probably reflect true changes, it is evident that their effects on the diet are not nearly so far-reaching as over a hard bottom.

To sum up, it may be said that over a hard bottom, *Mormyrus* eats larger kinds *and* larger individuals of prey species as its size increases. Over a soft bottom, which is characteristically a lacustrine habitat, such a change is not possible, and therefore chironomid, and to some extent chaoborid, larvae are eaten throughout. In addition, the consistent trend which emerges from these data is that the larger fishes become, the more they feed over mud, and the less over rocks and sand. This ontogenetic pattern supports the contention that *M. kannume* is of riverine origin but has become well-adapted to the most extreme of lake environments, where it can successfully maintain itself entirely on chironomid larvae. It also supports the view that in the lake the smallest *Mormyrus* inhabit rocky sites from which they disperse as they become larger. One consequence of this is that *M. kannume* differs markedly from a fish such as *Gasterosteus aculeatus* L. (Hynes, 1950) in that its food becomes less varied as it grows older.

No change with size is discernible in the proportion of fishes with stomachs empty or almost empty. In three of the habitats analyzed, there are more records of main contents in fishes 21 to 25 cm. long than in other size-groups, and this number declines progressively as fishes become larger. This indicates that larger fishes distribute their feeding effort more equitably amongst the items they eat.

Age of moon

Since the three most important items of its diet exhibit a lunar periodicity of development, it is to be expected that *Mormyrus* should show corresponding fluctuations in its food. That this does in fact take place was first demonstrated by Macdonald (1956), who showed that the sizes of chironomid and chaoborid larvae eaten by *M. kannume* are correlated closely with the age of the moon. Macdonald found that the species he studied complete a generation in two lunar months, but that two temporally separated populations co-exist, thus making available a constant food supply for *Mormyrus*. This I found also to be the case in *Povilla*, which completes a generation in four or five lunar

months, and of which a corresponding number of populations co-exist and are available for food (Corbet, 1957 b).

There is also lunar periodicity in the proportions of different species eaten. In Ekunu Bay, *M. kannume* feeds mainly on its preferred food, *Chironomus* larvae, when this is most abundant in the mud. But after an emergence (at new moon) the fishes revert to feeding mainly on *Tanypus* larvae, until such time as *Chironomus* becomes common once again. Thus, over mud, there is a *Tanypus—Chironomus* cycle of feeding (Macdonald, 1956).

Analysis of my own records for a hard bottom habitat confirms and amplifies these findings (Table 11). Data were grouped so that the lunar month was divided into six periods, such that new moon fell in the middle of the first and full moon in the middle of the fourth. Records for chironomid larvae as main contents fluctuated irregularly, but were fewest in period 2, that is, just after emergence. Chaoborid larvae only provided the main contents to an appreciable extent in period 4, which is the time when there is the greatest number of large larvae present. No periodicity was observed in the occurrence of *Povilla* larvae, but as main contents they were represented most in periods 3 and 4 (when larvae were largest) and least in 5 and 6 (after an emergence, when larvae were smallest, and eggs had not yet hatched).

TABLE 11

Mormyrus kannume: percentage main contents of three food items at different phases of the moon over a hard bottom.

	Lunar day group (New)			(Full)		
Food	1	2	3	4	5	6
Chironomid larvae	31	17	47	18	28	40
Chaoborid larvae	2	1	4	9	4	–
Povilla larvae	14	14	18	19	10	4
Number of fishes containing food	99	135	45	191	134	89
Number of days	5	9	4	14	10	9

Thus an overall fluctuation in importance of the three main food-types can be discerned, such that chironomid larvae reach a peak at new moon, and chaoborid and *Povilla* larvae at full moon.

Conclusions

In the Victoria Nile, and probably also Lake Victoria, small *M. kannume* live amongst rocks and stones and feed on the lithophilic insects there. In the lake the food of fishes over 15 cm. long consists almost entirely of insects, amongst which the most important items are larvae of chironomids, chaoborids, *Povilla*, free-living Ephemeroptera, Trichoptera and Odonata. *M. kannume* must be regarded as a facultative feeder in as much as the proportions of these

and less important items of food depend to a significant extent on its feeding ground and size, and on the age of the moon. Despite this, however, chironomid larvae comprise by far the most important food under nearly all combinations of circumstances. Even when eaten least (namely by fishes over 35 cm. long feeding over a hard bottom at full moon), they still provide the main contents in 18·3 per cent of fishes, a value exceeded only by that for *Povilla* larvae, which at 19·2 per cent are then at their peak. Chironomid larvae are eaten most over mixed or soft bottoms at new moon, when they usually occur in every fish and provide the main contents in about 80 per cent. It is generally true that by volume chironomid larvae are nearly always at least four times, and usually fifteen to twenty times, more important than any other insect, and it is evident that they must be the preferred food.

Alone amonst the mormyrids of Lake Victoria, *M. kannume* has successfully invaded and exploited the soft bottom habitat. In this connection it is interesting to note that in juvenile *Mormyrus* the shape of the head resembles that of *Marcusenius*, whereas the adults possess a long snout, suited for probing both among crannies or in mud. This ontogenetic change may reflect a modification of feeding habits in response to lacustrine conditions. One result of this is that potential intra-specific competition amongst older fishes for large insects over a hard bottom is much reduced. It is possible that this important adaptation may be in some measure responsible for the fact that *M. kannume* is probably the most abundant mormyrid in the lake.

M. kannume provides an important direct link between chironomid larvae and man, cormorants (Cott, 1952) and crocodiles (Cott, 1954).

PETROCEPHALUS CATOSTOMA CATOSTOMA (Günther)

This species has previously been known as *P. degeni* Blgr. (see Whitehead & Greenwood, 1959). Until recently it was known from only six specimens. Four of these (8 and 9 cm.) were collected in 1956 and 1957 from a marginal swamp pool in the Victoria Nile, 200 m. below the Owen Falls Dam ; all contained food.

Insects predominated in all stomachs, and chironomid larvae in two. Otherwise the food was varied, occurrences of the several items being : chironomid larvae (4) ; hydroptilid cases (3) ; larvae of *Povilla*, *Tricorythus*, free-living Ephemeroptera, *Phanostoma* and chironomid pupal breathing organs, Ostracoda and dead plant material (all 2) ; chaoborid larvae, Cladocera, Copepoda and Gastropoda (all 1).

As was the case with *Mormyrus macrocephalus* collected from the same site, the food was being obtained both from the river bed (*Tricorythus*, *Phanostoma*) and from marginal vegetation (plants, chaoborids). *P. catostoma* differs from *M. macrocephalus* in that all the organisms it eats are very small.

MARCUSENIUS NIGRICANS Boulenger

The habitat of this species appears to be fringes of papyrus swamp and marginal vegetation in lakes and rivers (Worthington, 1929 ; Greenwood, 1956 a). Specimens are seldom collected save in fish traps. Twelve fishes, all containing food have been examined.

Rivers

One fish (8 cm.) was caught in a kek in a large Kenya river (probably the Nzoia) in its middle reaches (P. J. P. Whitehead, personal communication). *Simulium* larvae formed the main contents. All other items were aquatic insects, namely larvae of chironomids, free-living Ephemeroptera, and Trichoptera, which included the hydropsychid *Cheumatopsyche falcifera*. In view of its possible significance as a predator of larval *Simulium*, further information concerning the feeding habits of *M. nigricans* in rivers would be of interest, although it is probably too rare to effect an appreciable measure of control.

Lakes

Eleven specimens were examined. Five (3–6 cm.) were caught with a hand-net near the surface of an artificial channel cut in papyrus swamp at Bugungu, near Jinja. A papyrus mat formed a bottom about 1 m. deep (G. S. Carter, personal communication). These fishes all contained insects. Chironomid larvae provided the main contents in four fishes and a small *Clarias* (*ca.* 25 mm.) in the other, which was itself only 5 cm. long. Other occurrences were : Ostracoda (3) ; *Povilla* larvae (2) ; larvae of Anisoptera and free-living Ephemeroptera, Hydracarina and *Caridina* (all 1).

Six fishes (8 and 9 cm.) were obtained from unspecified habitats in Lakes Victoria (3) and Nabugabo (3). The main contents in all was insects, two being chironomid and two *Povilla* larvae. Other occurrences were : chironomid larvae (6) ; *Povilla* larvae (4) ; chaoborid and hydroptilid larvae (both 1).

In swamps this species appears to be predominantly insectivorous and to feed mainly on chironomid larvae, but also to a significant extent on *Povilla*. Unless the specimen containing *Clarias* was atypical, it can be assumed that small fishes may sometimes supplement its normal diet of insects.

One specimen (*ca.* 5 cm.), probably of this species, was found in the stomach of a *Mormyrus macrocephalus* 51 cm. long which was caught near marginal swamp. In Lake Kyoga six out of seven *Lates* (*ca.* 38 cm.) were found to have been feeding on *Marcusenius*, probably *nigricans*, about 7 cm. long (D. H. Rhodes, personal communication).

MARCUSENIUS GRAHAMI Norman

Though said to be common in shallow coastal waters in Lake Victoria, especially over sand (Greenwood, 1956 a), this species is not well represented in gill-net catches—possibly because of its size, or perhaps because it seldom moves into open water. Specimens examined for food were derived as shown in Table 12.

Lake Victoria

In Table 13 records from all habitats in the lake have been combined, since the samples from mixed and soft bottoms are too small to merit separate analysis, and in any case differ very little from those from hard bottoms. Items represented *only* over a hard bottom are chaoborid and Anisoptera larvae, and those only over a soft bottom, Zygoptera larvae. Apart from this,

TABLE 12

Derivation of *Marcusenius grahami*.

	Lake Victoria			Victoria Nile	Other rivers	Totals
	HARD	MIXED	SOFT			
Numbers examined	23	1	10	158	8	200
Numbers containing food	22	1	10	152	8	193
Size-ranges (cm.)	13–16	16	14–16	3–15	11–15	3–16

TABLE 13

Marcusenius grahami : percentage occurrence and main contents in Lake Victoria.

Food	Occurrence	Main contents
Insects	97	95
Chironomid larvae	94	69
Chaoborid larvae	11	—
Povilla larvae	64	—
Ephemeroptera : free-living larvae	56	3
Anisoptera larvae	6	—
Trichoptera larvae	72	6
Phanostoma	6	—
Ecnomus	19	—
Hydroptilidae	56	6
Corixidae	17	—
Hydracarina	47	—
Ostracoda	14	—
Caridina	8	—
Gastropoda	19	6

the only apparent difference was that free-living Ephemeroptera larvae were commoner over a hard bottom.

In the lake, *M. grahami* is predominantly insectivorous, and chironomid larvae appear to constitute its only important food, although various other insects are eaten, and also Hydracarina, Ostracoda and Gastropoda. It feeds more on Corixidae (*Micronecta*) than do other mormyrids, and at times concentrates on Trichoptera larvae, especially hydroptilids. One fish (15 cm.) contained at least thirty-five larvae of the rheophilic leptocerid *Pseudoleptocerus schoutedeni*, and others had eaten *Hemileptocerus gregarius* in addition to those listed in Table 13. The *P. schoutedeni* larvae were found with and without their cases. The gastropods were represented by opercula only, and included *Melanoides*, *Gabbia* and *Bellamya*.

Victoria Nile

Fishes were derived mainly from a swamp pool, mentioned previously, below the Owen Falls Dam. Few came from the river bed. All but two of the fishes were collected on or after 13th June 1956, a date by which the lithophilic river fauna had almost returned to normal after DDT treatment (see Corbet,

1958 a). The only two items noted then as not having yet reached a stable density were larvae of free-living Ephemeroptera and of *Afronurus ugandanus*, both of which were however present and being eaten by *Mastacembelus victoriae*—a specialized feeder on lithophilic insects.

TABLE 14

Marcusenius grahami : percentage occurrence and main contents in Victoria Nile.

Food	Occurrence	Main contents
Insects	100·0	—
Chironomid larvae	84·9	27·6
Chaoborid larvae	3·3	—
Povilla larvae	36·8	—
Ephemeroptera : free-living larvae	8·6	—
Tricorythus larvae	12·5	—
Trichoptera larvae	70·4	5·9
Phanostoma	57·2	0·7
Ecnomus	2·0	—
Hydroptilidae	67·1	5·3
Tipulidae : larvae and pupae	73·7	21·7
Hydracarina	28·3	—
Ostracoda	28·3	0·7
Gastropoda	23·7	—
Plants, dead	35·5	6·6

As in the lake, chironomid larvae were the most important food, but almost a third of the river fishes had also fed heavily on larvae and pupae of tipulids. Also many of them had much plant debris in the stomach.

The only occasion on which fishes less than 11 cm. long were caught was on 25th July, 1957, 447 days after the last DDT treatment. Fishes on this day fell into two size-groups, the food of which is compared in Table 15.

TABLE 15

Marcusenius grahami : occurrence and (main contents) in the Victoria Nile.

Food	Size-group in cm.	
	3–6	12–14
Chironomid larvae	16 (7)	13 (3)
Ephemeroptera : free-living larvae	7	3
Hydracarina	12 (1)	3
Ostracoda	10 (1)	2
Tricorythus larvae	4	4
Hydroptilid larvae	2	12 (3)
Phanostoma larvae	1	11
Tipulid larvae/pupae	0	10
Number of fishes containing food	16	13

Even from this small sample it is evident that marked differences exist between the small and large fishes. Thus small fishes in this habitat had eaten more Ostracoda and Hydracarina than had large fishes, and probably more free-living Ephemeroptera larvae, whereas large fishes had eaten more hydroptilids, *Phanostoma* and tipulids. These differences may result merely from the fishes eating larger prey as they themselves grow larger—a phenomenon already noted in *Mormyrus kannume*. *Phanostoma* larvae, for instance, would probably not be available to the smallest fishes on account of their size. The full implications of Table 15 will not be understood until more is known of the microhabitats occupied by the food organisms concerned.

The Trichoptera eaten included *Pseudoleptocerus schoutedeni* and *Cheumatopsyche copiosa*. The latter, probably a reliable indicator of rheophilic conditions, occurred in three fishes (5 and 13 cm.) ; this suggests that some river-bed feeding occurs throughout the size-range studied. This is supported by the presence of a pupa of *Simulium alcocki* in a fish of 13 cm. Gastropods recognized were *Biomphalaria* and *Melanoides*, the latter being represented, as in the lake, by opercula. Many of the Ostracoda and Hydracarina in the stomachs of small fishes (captured in mid-morning) were alive. Other food included fragments of a spider and an earwig (Dermaptera).

Other rivers

The food of eight fishes from other rivers (Kagera and Nzoia) closely resembled that observed in the Victoria Nile. Chironomid larvae formed the principal food, and Trichoptera were also important. Other food included almost all items encountered in fishes from the Victoria Nile, with a few additions, namely, the pelecypod *Corbicula africana*, a corixid larva, a terrestrial beetle, and the egg of an endophytic dragonfly. As before, operculate gastropods were represented only by their opercula, and one fish contained *Simulium* larvae.

Conclusions

Chironomid larvae undoubtedly comprise the preferred food of *M. grahami*, whether in rivers or the lake. Amongst the items of minor importance, Trichoptera and Gastropoda are prominent. The latter are apparently selected as food—rather than ingested fortuitously—since they are represented almost always by opercula.

Although some items of its diet are definitely rheophilic (*Tricorythus*, *Phanostoma*, *Simulium*), the presence of plant debris, *Ecnomus* larvae and corixids indicates that much feeding occurs in sheltered sites also. It seems likely that *M. grahami* obtains its food in places where there is considerable water movement, but where there is also adjacent shelter. In the lake such sites would be found at the edge of marginal vegetation on exposed shores, and in rivers where natural obstacles check the flow sufficiently to allow eddies to form and emergent vegetation to grow at the water's edge. Thus in its feeding habits *M. grahami* might be termed an interface species. Small and large fishes show this behaviour and differ only in the size of prey they ingest.

GNATHONEMUS LONGIBARBIS Hilgendorf

In Lake Victoria this species occurs sparingly in shallow inshore waters over sandy and rocky shores (Graham, 1929 ; E.A.F.R.O., unpublished), a distribution reflected by the values given in Table 16. Although samples

TABLE 16

Derivation of *Gnathonemus longibarbis*.

	Lake Victoria			Victoria Nile	Other rivers	Totals
	HARD	MIXED	SOFT			
Numbers examined	66	17	24	83	5	195
Numbers containing food	61	17	22	83	5	188
Size-range (cm.)	17–35	18–36	13–32	11–21	11–23	11–36

from any but a hard bottom are small, the results for the three types of habitat have been presented separately, since they are consistent enough to confirm similar trends observed in other mormyrids.

Lake Victoria

Five fishes examined by Graham (1929) all contained "insects". My sample (Tables 17 and 18) shows that *G. longibarbis* is predominantly insectivorous, and that only three foods are of regular importance to it—chironomid, *Povilla* and Odonata larvae. The remaining items in a very varied diet rarely achieve the status of main contents, and then usually over a hard bottom where

TABLE 17

Gnathonemus longibarbis : percentage occurrence in Lake Victoria.

Food	HARD	MIXED	SOFT
Insecta	100	100	100
Chironomid larvae	80	82	86
Chironomid pupae	5	12	18
Chaoborid larvae	2	12	—
Culicine larvae	—	—	14
Povilla larvae	67	100	91
Ephemeroptera : burrowing larvae	3	—	—
Ephemeroptera : free-living larvae	46	—	27
Anisoptera larvae	25	59	55
Trichoptera larvae	44	24	18
Ecnomus	26	—	9
Hydroptilidae	11	12	14
Hydracarina	33	53	32
Ostracoda	21	6	23
Caridina	7	—	9
Oligochaeta (*Alma*)	2	—	—
Gastropoda	13	12	9
Fish eggs	—	—	9

TABLE 18

Gnathonemus longibarbis : percentage main contents in Lake Victoria.

Food	HARD	MIXED	SOFT
Insects	97	100	95
Chironomid larvae	30	35	32
Chironomid pupae	—	—	5
Povilla larvae	18	35	18
Ephemeroptera : burrowing larvae	3	—	—
Ephemeroptera : free-living larvae	3	—	—
Anisoptera larvae	10	18	23
Trichoptera larvae	2	—	—
Hydroptilidae	2	—	—
Caridina	—	—	5
Oligochaeta (*Alma*)	2	—	—

the food in any case tends to be most diverse. The hard bottom diet, as in other mormyrids, contains more larvae of free-living and burrowing Ephemeroptera, and Trichoptera.

Chironomid larvae appear to be about 1½ times as important as *Povilla* larvae, which in their turn exceed Odonata larvae by about the same amount. The Odonata larvae, which comprise both Anisoptera and Zygoptera, consist very largely of Libellulidae, amongst which *Trithemis* predominates. Burrowing Ephemeroptera (over sand) included *Eatonica schoutedeni* and *Ephemera* (presumably *E. aequatorialis*). Trichoptera included larvae of *Pseudoleptocerus schoutedeni* and pupae of *Dipseudopsis capensis* Walker. One fish contained a larva of the stone-fly, *Neoperla spio*. Gastropoda were represented by both shells (*Bellamya, Gyraulus, Biomphalaria, Segmentorbis angustus*) and opercula (*Melanoides, Bellamya*) ; the shells were almost always empty and eroded, and therefore probably derived accidentally from bottom deposits. The only fish remains were eggs, one lot being non-cichlid. Crustacea eaten included Conchostraca (4 fishes). The culicine larvae and aquatic beetles would have been obtained in or near marginal vegetation.

Victoria Nile

Fishes were caught in the swamp pool and on the river bed at the site 200 m. below the Owen Falls Dam. Of the eighty-three examined, twenty-four were obtained in March and April, 1956, when the fauna of the river bed was still affected by DDT treatment. Corresponding changes in feeding behaviour during this period were noted in *Gnathonemus longibarbis* (Corbet, 1958 a), and have been summarized in Table 19. Accordingly an assessment of the normal diet in this habitat has been based on fifty-nine fishes collected at times when the river was unaffected by DDT (Table 19).

In the river the fishes were smaller than those examined from the lake, and did not show the same feeding habits. Chironomid larvae still provided the most important food, but only in about half as many individuals, whereas the only other item of more than occasional importance was hydroptilid larvae. *Povilla* and Odonata larvae, though often eaten, were of minor importance by volume. A number of fishes contained plant debris and so presumably had been feeding in sheltered marginal sites or in swamp.

TABLE 19

Gnathonemus longibarbis : percentage occurrence and (main contents) in Victoria Nile, showing effects of DDT treatment.

Food	Normal	During treatment
Insects	100	96
Chironomid larvae	83 (29)	46 (8)
Chironomid pupae	14	—
Chaoborid larvae	9	13
Povilla larvae	49	50
Ephemeroptera : free-living larvae	37	—
Tricorythus larvae	32 (3)	—
Anisoptera larvae	14	17
Zygoptera larvae	9	8
Trichoptera larvae	61 (20)	33 (4)
Phanostoma	27 (2)	8
Hydroptilidae	53 (19)	29 (4)
Coleoptera	9	8
Hydracarina	15	21
Ostracoda	48	38
Gastropoda	15	33
Plants, dead	36 (12)	92 (67)
Numbers containing food	59	24

Ephemeroptera larvae included *Afronurus ugandanus* and *Euthraulus*, which are typically lithophilic forms. One fish contained the egg of an endophytic dragonfly, presumably Zygoptera. Two contained *Simulium* larvae and pupae, respectively, and one tipulid larvae. Gastropoda identified were *Gyraulus costulatus*, *Segmentorbis augustus* and *Biomphalaria*, and there was one small pelecypod. One individual contained Conchostraca. Occasional terrestrial insects showed that some surface feeding had occurred.

It is clear that in this habitat *G. longibarbis* spreads its feeding effort fairly evenly between the stones of the river bed and sites in sheltered marginal vegetation or swamp. It is thus well adapted to withstand changes such as those it experienced during the DDT treatment. At that time it appeared that (Table 19) profitless attempts had been made to obtain food from the river bed (as evidenced by sand grains), but that most feeding had occurred in sites sufficiently sheltered to permit accumulation of plant debris and silt.

Although numbers for comparison are small, there are nevertheless indications that within the size-range studied the occurrence of certain items changes with size. *Tricorythus* larvae and Hydracarina seem to be eaten more by smaller fishes and Odonata larvae and plant debris more by larger ones. Such changes would be consistent with a tendency for larger fishes to eat larger prey and to feed less in exposed situations. The changes observed, though similar, are not so well marked as in *Marcusenius grahami*, but an explanation for this could be the absence of any fishes less than 10 cm. long in the present sample.

Other rivers

Five fishes from other rivers (Kagera, Sondu) contained food very similar to that observed in the Victoria Nile. Two fishes (14 cm.) had eaten *Simulium* larvae and a larva of the scarce lithophilic mayfly, *Prosopistoma* (see Gillies, 1954). Other mayfly larvae were *Polymitarcys savignyi*? (Kagera) and *Eatonica schoutedeni* (Sondu).

Conclusions

G. longibarbis is almost entirely insectivorous. Every fish examined, which contained food, had eaten insects, although a small number had also fed on other arthropods, oligochaetes and fish eggs.

In the lake three types of insects between them provide the main food—chironomid, *Povilla* and Odonata larvae. The importance of the first two probably means that *G. longibarbis* resembles *Mormyrus kannume* in showing a lunar periodicity in the food it eats. In the ninety-seven fishes examined from the lake, no other food items provided the main contents in more than 2 per cent.

Although *G. longibarbis* feeds both on the bottom (often sand) and in marginal vegetation, in the lake it frequents less exposed sites than does *Marcusenius grahami*, but at the same time feeds less in vegetation. In rivers, however, typically rheophilic insects may be eaten, especially by smaller fishes, and these may on occasion include larvae and pupae of *Simulium*.

The water-snake, *Grayia smythii* (Leach), has been noted as a predator of *G. longibarbis* amongst rocks on the bed of the Victoria Nile.

GNATHONEMUS VICTORIAE Worthington

The habitat of this species in Lakes Victoria and Kyoga is said to be the same as that of *G. longibarbis* (Greenwood, 1956 a ; Worthington, 1929).

TABLE 20

Derivation of *Gnathonemus victoriae*.

	Lake Victoria			Victoria Nile	Other rivers	Totals
	HARD	MIXED	SOFT			
Numbers examined	51	177	177	249	5	659
Numbers containing food	51	176	177	243	5	652
Size-ranges (cm.)	15–22	16–22	17–26	14–23	13–16	13–26

Lake Victoria

The six fishes examined by Graham (1929) all contained insects and at least one of them, chironomid larvae. It is clear from Tables 21 and 22 that in Lake Victoria *G. victoriae* is predominantly insectivorous and that, of the many items in its diet, only chironomid larvae are consistently important. These predominate as food in all habitats, and to approximately the same

TABLE 21

Gnathonemus victoriae : percentage occurrence in Lake Victoria.

Food	HARD	MIXED	SOFT
Insects	98	100·0	98·3
Chironomid larvae	92	97·2	96·6
Chironomid pupae	4	14·2	18·6
Chaoborid larvae	8	15·3	6·8
Culicine larvae	—	—	10·2
Povilla larvae	39	65·9	43·5
Ephemeroptera : burrowing larvae	2	—	—
Ephemeroptera : free-living larvae	14	11·4	19·8
Tricorythus larvae	2	—	—
Anisoptera larvae	8	10·8	18·6
Trichoptera larvae	24	34·1	24·3
Ecnomus	4	2·3	0·6
Hydroptilidae	16	28·4	24·3
Coleoptera	6	5·1	32·2
Hydracarina	49	68·2	67·2
Ostracoda	53	80·1	82·5
Conchostraca	—	10·8	6·2
Caridina	—	2·8	6·2
Molluscs	10	13·3	10·7
Gastropoda	4	13·1	10·7
Pelecypoda	8	—	—
Fish eggs	6	1·1	2·8

TABLE 22

Gnathonemus victoriae : percentage main contents in Lake Victoria.

Food	HARD	MIXED	SOFT
Insects	98	93·8	92·7
Chironomid larvae	47	53·4	45·2
Chironomid pupae	—	—	2·3
Culicine larvae	—	—	1·1
Povilla larvae	6	9·1	—
Ephemeroptera : burrowing larvae	2	—	—
Anisoptera larvae	—	1·1	—
Trichoptera larvae	—	0·6	—
Hydroptilidae	—	0·6	—
Hydracarina	—	1·7	1·1
Ostracoda	2	4·5	6·2

extent in each, being about seven times as important by volume as the only other items providing the main contents in an appreciable number of fishes—namely *Povilla* larvae and Ostracoda.

Although in Tables 21 and 22 data from the three habitat types have been analyzed separately, a rigorous comparison is not permissible. This is because firstly, the hard bottom sample is small, and secondly, all but seven of the soft bottom fishes came from one anomalous habitat under atypical circumstances. Though soft by definition, this habitat (Fisherman's Point, Jinja) is on the edge of marginal swamp and yet at the same time not far from exposed

sites in Napoleon Gulf. Furthermore, the fishes appeared sporadically in large numbers, rather than regularly over a long period, and may therefore have been undergoing unusual movements at the time. At all events it is clear that much of the food had been obtained from exposed habitats, whereas the presence of culicine larvae and Coleoptera shows that some feeding at any rate had occurred in marginal vegetation.

The burrowing mayfly larva eaten was *Eatonica schoutedeni*. Odonata larvae, with a single exception (*Ceriagrion* sp.), were all Libellulidae and mostly *Trithemis*. Coleoptera identified were *Hydrovatus longicornis* Sharp. and *Hydrocoptus koppi* Welm. Trichoptera included a larva of *Hemileptocerus gregarius* and a pupa of *Dipseudopsis capensis*. Gastropods (represented by shells) included *Bellamya*, *Gabbia*, *Biomphalaria*, *Bulinus*, *Gyraulus* and *Segmentorbis* ; one pelecypod was *Sphaerium*. With the exception of one individual (20 cm.) which contained very small fish fragments, all fish prey was represented by eggs. In the four cases recognized, the eggs were non-cichlid (two probably cyprinid) and contained embryos.

In a large sample of fishes from the soft bottom habitat mentioned above, no significant changes of food with size could be discerned. Even the largest fishes (22 cm.) fed just as heavily as others on the smallest items, such as Ostracoda and Hydracarina. In this respect *G. victoriae* differs from certain other mormyrids (e.g. *Mormyrus kannume*, *Gnathonemus longibarbis*) which eat these items less as they grow larger. This difference may indicate an incipient specialization towards a feeding preference for Ostracoda and Hydracarina. The fact that such small animals as these sometimes provide the main contents, means that at times *G. victoriae* must feed extremely heavily on them.

Victoria Nile

Fishes were caught mainly in the swamp pool 200 m. below the Owen Falls Dam, where *G. victoriae* was the species represented most in collections. Of the 243 fishes containing food, only twenty were collected when the river fauna was unaffected by DDT treatment. As the feeding habits of these twenty fishes were very consistent, it may be assumed that they provide a reliable index of the normal food in this habitat. The two other samples are compared with them in Table 23, from which it is clear that normally most food was obtained from the surfaces of stones, as indicated by the incidence of lithophilic types such as larvae of *Tricorythus*, *Afronurus*, *Euthraulus*, *Neoperla spio* (Plecoptera) and *Metacnemis valida* (Zygoptera). These were evidently reducing the relative importance of chironomid larvae as prey. When subjected to the effects of DDT, fishes fed considerably more in sheltered sites, as shown particularly by the presence of plant debris.

Fish remains (represented by a single rib or fin-ray) were found in only one individual (17 cm.) on 16 March 1956, whereas eggs (probably of fishes) occurred twice. Other items noted only in one or two fishes were the hydropsychid *Cheumatopsyche copiosa*, culicine larvae, Copepoda and Conchostraca. All gastropod shells were *Biomphalaria* ; and the Odonata included Libellulidae (probably *Trithemis donaldsoni* Calvert) and *Coenagrion*.

TABLE 23

Gnathonemus victoriae : percentage occurrence and (main contents) in Victoria Nile during and after DDT treatment

Food	During treatment	40–49 days after last treatment	447 days after last treatment
Insects	85	97	100
Chironomid larvae	76 (20)	87 (23)	100 (10)
Chironomid pupae	6	14	35
Chaoborid larvae	5	5	5
Povilla larvae	44 (1)	33 (2)	50 (5)
Ephemeroptera : free-living larvae	2	4	90
Tricorythus larvae	2	1	60
Anisoptera larvae	4	6 (1)	—
Zygoptera larvae	—	2 (1)	15
Trichoptera larvae	18	16	70
Phanostoma	1	7	5
Ecnomus	—	1	45
Hydroptilidae	16	10	35
Coleoptera	13	11 (1)	10
Hydracarina	46 (5)	18	30
Ostracoda	86 (8)	76 (8)	60
Gastropoda	17	33	20
Plants, dead	89 (41)	33 (4)	5
Sand grains	10	21	25
Numbers containing food	97	126	20

Other rivers

The food of five fishes from the Sondu River, Kenya, resembled that eaten in Lake Victoria rather than in the Victoria Nile, possibly because these fishes came from the middle reaches where water movement is less vigorous.

Conclusions

G. victoriae is exceptional amongst Mormyridae in so far as even large fishes eat significant numbers of Ostracoda, Hydracarina and Conchostraca. So heavily do fishes feed on these items that they sometimes achieve the status of main contents. Despite this habit, *G. victoriae* is predominantly insectivorous : only four of 404 fishes containing food in the lake were without insect remains in the stomach.

Although the diet of fishes in the lake is varied, chironomid larvae provide the only important food, occurring as they do in 92–97 per cent and providing the main contents in 45–53 per cent. But under normal conditions in rivers their importance is offset by lithophilic insects which are eaten extensively.

G. victoriae is an adaptable and generalized feeder. When deprived of lithophilic insects, whether by DDT or lacustrine conditions, it readily obtains food from more sheltered sites and exploits chironomid larvae, Ostracoda and Hydracarina to an increasing extent. But it may be noted that in the lake, even individuals which have fed in marginal vegetation have often obtained

some of their food also from exposed sites. A knowledge of the species of Ostracoda and Hydracarina eaten and of their microhabitats is essential if the feeding habits of *G. victoriae* are to be well understood.

DISCUSSION : MORMYRIDAE

It is characteristic of mormyrids to feed on insects and small invertebrates which they obtain, usually from the bottom, often amongst vegetation, but hardly ever from the water surface. As feeders on small organisms they ingest large quantities of food daily, and their stomachs are very seldom empty (Table 59). With certain exceptions, which include *Gnathonemus victoriae* and mud-feeding *Mormyrus kannume*, the several species show a tendency towards economy of feeding effort in that they eat larger kinds *and* larger individuals of prey as they themselves grow larger. This behaviour is most pronounced in *Mormyrus macrocephalus* and *Gnathonemus longibarbis*.

The size of animals and the spatial position they occupy in a habitat seem to dictate their importance as prey. Thus, within the limits these conditions impose, the food eaten is a direct reflection of the bottom fauna of the habitat in which a fish feeds. This circumstance, together with the fact that the same groups of prey are represented in almost all species, makes it very difficult to discern trophic divergence in members of this family. It is in just such a case as this that the ' occurrence ' method of food appraisal is inadequate by itself, and requires a second measure, largely independent of it, to amplify and confirm its verdict. The ' main contents ' criterion has therefore proved particularly informative in this family.

It happens that this study of the Mormyridae provides an unusually clear illustration of how misleading assessments of food preferences can be if based on a few specimens of uncertain provenance. For *Mormyrus kannume* it has been demonstrated that the proportions of the main items in its diet depend to a large extent on the size of fish, the feeding ground, and the age of the moon. Thus it can happen that large individuals feeding over a hard bottom at full moon can differ more in their food from other *M. kannume* than from certain other species. This example should be a sufficient caution against assessing food (not to mention preferences) on the examination of a few specimens localized in space or time.

It is consistent with the supposed origin of the lake icthyofauna that the mormyrids should be well adapted for life in riverine conditions. In the three species for which adequate juvenile material was available, the smallest fishes fed by preference on lithophilic insects living in very exposed sites on the river bed. Thereafter there was a well-marked tendency for fishes to feed in marginal and more sheltered situations as they grew larger. In *Mormyrus kannume* and *Marcusenius grahami*, for example, there was a fairly abrupt change in feeding behaviour when fishes reached a length of about 10 cm. Before this their diet had consisted mainly of rheophilic forms like *Tricorythus* and *Cheumatopsyche*, whereas subsequently it was dominated by chironomid larvae. This age-dependent change in feeding habits, so well-marked in the river, can still be discerned in the lake amongst larger fishes. In *Mormyrus kannume* its persistence can be recognized in the progressively

decreasing extent to which fishes over 17 cm. long feed on lithophilic insects. Since it is extremely unlikely that fishes in river and lake would differ in so fundamental a respect, this has provided the basis for the suggestion that juveniles of certain Lake Victoria mormyrids may live amongst the rocky regions of exposed shores.

The riverine derivation of the mormyrids could provide the key to an understanding of their ecology in the lake. It may be observed that in Lake Victoria all species save one have kept mainly to the lacustrine equivalents of their riverine habitats. The single exception, *Mormyrus kannume*, has extended the spectrum of its feeding behaviour to include organisms living in mud. This represents a distinct adaptation towards lacustrine conditions, and has probably made this species the most efficient and versatile bottom feeder in the lake.

The remaining species feed mainly over sandy bottoms (*Gnathonemus longibarbis*), in or near marginal vegetation (*Petrocephalus catostoma*, *Marcusenius nigricans*, *Mormyrus macrocephalus*), or both (*Marcusenius grahami*).

Mormyrus macrocephalus stands apart from the rest in being the only species in which small fishes form an important food of adults, and in which chironomid larvae do not predominate. It is the largest species and concentrates on the largest prey—a trend shown also by *Mormyrops* in Lake Tumba (Marlier, 1958). *Marcusenius nigricans* may also utilize fishes in marginal vegetation, but is otherwise typical of the family.

The six chironomid-eating species are likely to exhibit a lunar periodicity in feeding behaviour, and this will probably be most pronounced in *Mormyrus kannume*, and the two species of *Gnathonemus*, in which *Povilla* is also an important food.

The differences between the species are shown in Fig. 12. *Mormyrus kannume* has already been discussed, and the two swamp-dwelling species, *P. catostoma* and *Marcusenius nigricans*, are not well enough represented for preferences to be deduced, although the indication of a piscivorous habit in the latter is noteworthy.

Marcusenius grahami is an interface feeder in which Trichoptera and Gastropoda emerge as slightly more important than other foods. The Gastropoda are apparently eaten selectively and therefore probably represent the more significant line of potential specialization.

Gnathonemus longibarbis feeds slightly in vegetation but largely over a hard bottom. This, coupled with a tendency to concentrate on larger insects, means that *Povilla* and Anisoptera larvae are more important to it than to any other mormyrid in the lake. In its preference for Anisoptera it resembles *Mormyrus macrocephalus*, which however tends to feed more in vegetation.

Gnathonemus victoriae eats much smaller organisms and is possibly beginning to become specialized in this direction, since it shows a preference for Ostracoda, and even when large shows no sign of eating significantly larger prey.

The differences noted above are by no means as great as might reasonably be expected in a group of species actively competing with each other for food. Indeed, for reasons which will be given later (p. 92), it is very probable that

no effective interspecific competition for food exists amongst fishes in the lake. One of the main factors of importance to mormyrids in this respect is that their main food is probably super-abundant. In Lake Victoria, with the exception of *Mormyrus kannume*, no mormyrid seems abundant, and yet these and a few species of *Haplochromis* are almost the only species which, as adults, concentrate on a vast benthic insect fauna. The importance of Mormyridae in utilizing benthic insects has been emphasized by Verbeke

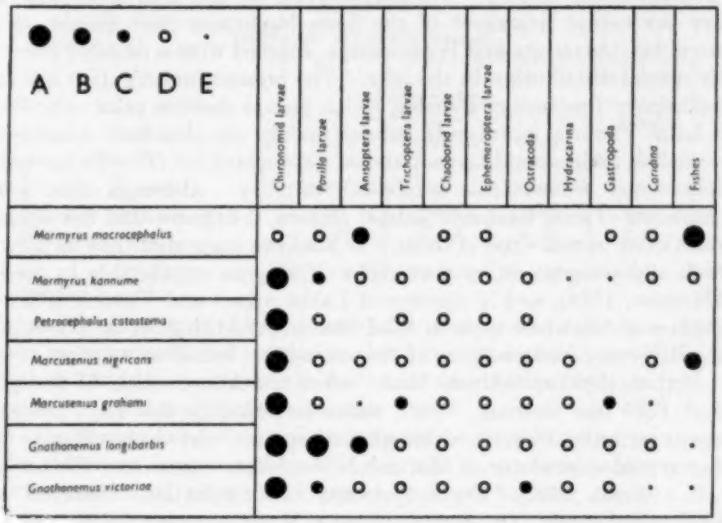


Fig. 12.—Mormyridae. Food preferences as shown by five grades of incidence for the main items. Data are from Lake Victoria except for *Petrocephalus catostoma catostoma* (Victoria Nile).

A. Main contents in 30 per cent or more.

B. Main contents in 10–29 per cent.

C. Main contents in 5–9 per cent.

D. Main contents in less than 5 per cent and/or occurrence in 10 per cent or more.

E. Occurrence in 5–9 per cent.

(1957 b) in his comparison of Lakes Kivu and Edward. In Kivu, where there are no mormyrids, *Povilla* larvae are abundant in a wide variety of microhabitats, but are eaten only occasionally and in small quantities (by *Barbus altianalis*), whereas in Edward they are eaten extensively by the several indigenous species of Mormyridae. It should also be noted that in Lake Victoria, as in Lake Edward (Verbeke, 1957 a), mormyrids are the only large fishes which eat substantial numbers of chaoborid larvae. In Lake Victoria, as we have seen, chaoborid larvae are only eaten in quantity by larger *M. kannume*.

The data presented here are inadequate for an assessment of competition in one important respect. The food categories recognized in this study,

although as refined as such categories usually are, may be too coarse to reveal real and informative differences in feeding behaviour. For example, no distinction has been made here between the different species of chironomid larvae, although many exist in the lake, and it is certain that the niches they occupy are diverse. Thus the observation that two fishes feed to the same extent on " chironomid larvae " may obscure important differences between them, to be discerned only when the species of larvae can be identified and their microhabitats defined. Further progress in this field must now await effective taxonomic treatment of the more important prey groups, such as Chironomidae, Ostracoda and Hydracarina, coupled with a detailed knowledge of their spatial distribution in the lake. The present investigation has served the preliminary function of showing which groups deserve prior attention.

In Lake Victoria mormyrids subsist mainly on abundant consumers of organic debris (chironomid larvae) and of phytoplankton (*Povilla* larvae), and therefore enjoy considerable ecological stability. Although they convert great amounts of such food into animal protein, it appears that few secondary predators exist to make use of them. It has been suggested that its unusually oily flesh and pungent odour may make *Mormyrus* unpalatable to predators (Worthington, 1929), and in surveys of Lakes Albert and Victoria it has been classified as a terminus type in food chains (Worthington & Worthington, 1933). However, food analyses of the crocodile, *Crocodilus niloticus* L. (Cott, 1954 ; Corbet, 1960 a) indicate that, before the introduction of the gill-net in about 1905 (see Graham, 1929), this was probably the main predator of *Mormyrus* in Lake Victoria although perhaps not elsewhere (Hippel, 1946). Another recorded predator of this fish is the larger cormorant, *Phalacrocorax carbo* (L.) (Cott, 1952). Fryer (personal communication) observed a fish eagle, *Cuncuma vocifer* (Daudin), carrying a *Mormyrus* near Jinja ; and I have seen a monitor lizard, *Varanus niloticus* L., at the Ripon Falls with a *Mormyrus* in its mouth ; but in neither of these cases could it be certain that the fish had been taken alive. Nowadays, man is probably the most significant predator of *M. kannume*, despite the diverse taboos which prohibit its consumption in certain places (see Graham, 1929 ; Greenwood, 1956 a). As pointed out by Graham (1929), this fish could provide a valuable and stable source of human food if exploited fully.

One additional respect in which mormyrids may affect man ecologically is as predators of *Simulium*. In this study only fifteen specimens of mormyrids were examined from rivers where *Simulium* occurred commonly, yet three of these contained larvae or pupae, and altogether four species (*Mormyrus kannume*, *Marcusenius nigricans*, *Marcusenius grahami* and *Gnathonemus longibarbis*) have been discovered to feed on *Simulium* in rivers. Apart from *Varicorhinus tanganicae* Blgr. (Marlier, 1952) and *Phractura ansorgei* Blgr. (Crisp, 1956), few other species have been found to prey on *Simulium* in Africa (see p. 90) ; it may be that mormyrids are important amongst them.

Finally, it should be mentioned that the productivity of lakes with a large benthic insect fauna but no mormyrids might benefit greatly from their introduction (see Verbeke, 1957 b), since these fishes are by far the most efficient exploiters of such food in African lakes.

CHARACIDAE

ALESTES JACKSONI Boulenger

This species was known previously as *A. nurse* (Rüppell) (see Greenwood, 1959 a). *A. jacksoni* is common in shallow coastal areas of Lake Victoria, in water less than 20 m. deep (see Greenwood, 1956 a). It is often caught in beach seines as well as gill-nets. Specimens examined for food were derived as in Table 24.

TABLE 24

Derivation of *Alestes jacksoni*.

	Lake Victoria			Totals
	HARD	MIXED	SOFT	
Numbers examined	66	286	265	617
Numbers containing food	60	246	239	545
Size-ranges (cm.)	7–21	12–20	8–21	7–21

Lake Victoria

Graham (1929) found plants, insects, fish and molluscs in the twenty-one stomachs he examined, and concluded that the diet was varied. The present data (Tables 25 and 26) confirm this, but reveal that the food consists principally of three items : insects, plants and fishes.

That the insects are taken mainly from the surface of the water is evident from the relatively large numbers of terrestrial forms in the diet, and from the predominance of chironomid pupae and adults over larvae. In this respect the diet contrasts strongly with that of a bottom-feeder such as *Mormyrus kannume*, which eats many of the same items, but in different proportions (Tables 8 and 9). In *A. jacksoni* the relative numbers of *Povilla* larvae and adults (see especially Table 26) are consistent with a surface-feeding habit, since free-swimming larvae are constantly available, whereas adults emerge on only a few days each lunar month. Here it may be remarked that the *Povilla* larvae in stomachs are not associated with silken cases ; and also that the presence of imagines and sub-imagines indicates that surface-feeding occurred within about an hour of sunset. It has already been noted (Corbet, 1957 b) that at certain times emerging *Povilla* may comprise the sole contents of stomachs. The same is often true of teneral adults and pupal exuviae of chironomids and chaoborids, except that the latter are associated with new, instead of with full moon (Fig. 13). There is therefore a lunar periodicity in feeding which involves first chironomids and chaoborids, and then *Povilla*. In this respect *A. jacksoni* resembles certain mormyrids, except that, because it is utilizing the surface and not the benthic phase of the insects, the periodicity is more clearly defined. Chaoborids identified from stomachs (within 7 days of new moon) include *Chaoborus pallidipes* Theo. and *C. anomalus*. Trichoptera are also taken as pupae or adults at emergence, probably at about sunset (see Corbet and Tjønneland, 1955) ; species eaten include *Athripsodes stigma* Kimmins, *A. ugandanus* Kimmins and *Ecnomus kunenensis* Barnard.

TABLE 25

Alestes jacksoni : percentage occurrence in Lake Victoria.

Food	HARD	MIXED	SOFT
Insects	90	79·3	46·0
Chironomid larvae	8	1·6	2·5
Chaoborid larvae	5	1·2	0·8
Povilla larvae	15	6·5	6·7
Ephemeroptera : free-living larvae	3	—	3·3
Anisoptera larvae	18	6·1	7·9
Zygoptera larvae	—	0·8	—
Corixidae	2	3·3	2·5
Trichoptera larvae	3	0·8	0·8
Hydracarina	2	0·4	—
Ostracoda	—	2·8	—
Caridina	—	—	0·4
Potamon	—	0·8	0·4
Molluscs	10	3·3	5·4
Gastropoda	8	3·3	5·4
Pelecypoda	3	—	—
Fishes	10	34·6	9·2
Cichlidae	5	18·3	5·4
Haplochromis	2	11·0	3·8
Tilapia	—	0·4	—
Non-cichlids	—	2·0	0·8
Engraulicypris	—	2·0	0·8
Plants	45	51·2	86·6
Plants, living	17	40·2	80·3
bitten	12	27·6	39·3
Sand grains	11	0·3	0·8
Surface forms			
Chironomid pupae	17	35·4	11·7
Chironomid adults	20	17·9	15·5
Povilla adults	2	2·8	3·3
Ephemeroptera adults	7	1·2	1·7
Trichoptera pupae	2	0·4	5·9
Terrestrial insects	53	37·4	11·3
Isoptera	2	17·5	2·5
Hymenoptera	27	15·9	5·9

Amongst terrestrial insects eaten, the most important are Hymenoptera (probably mainly camponotine ants) and Isoptera, which include *Macrotermes bellicosus* (Smenth.) and *M. natalensis* (Hav.). The latter are said to emerge between midnight and dawn (Harris, personal communication). Other insects taken are Orthoptera (Mantidae : *Polyspilota aeruginosa* (Goeze) ; and Gryllidae) and Lepidoptera (Noctuidae). Other occasional items which indicate surface feeding are feathers and fragments of charcoal.

The few insects definitely taken below the surface are almost entirely Anisoptera larvae, some of which (unlike those eaten by *Mormyrus kannume*) are bitten before being ingested. These consist mainly of Libellulidae (*Trithemis, Brachythemis*) and *Ictinogomphus ferox*. Very few of the larvae eaten were either in the final instar or pharate, and therefore were taken mainly from the bottom, possibly when plant-feeding was taking place. It may be

TABLE 26

Alestes jacksoni: percentage main contents in Lake Victoria.

Food	HARD	MIXED	SOFT
Insects	58	35·0	12·6
Povilla larvae	—	1·2	—
Anisoptera larvae	13	3·7	2·5
Molluscs	5	—	0·8
Gastropoda	3	—	0·8
Pelecypoda	2	—	0·8
Fishes	3	20·3	4·6
Cichlidae	3	11·8	4·2
Haplochromis	2	6·9	2·5
Tilapia	—	0·4	—
Non-cichlids	—	1·2	0·4
Engraulicypris	—	1·2	0·4
Plants	17	21·1	57·3
Plants, living	13	18·7	54·5
bitten	3	3·3	10·5
Surface forms			
Chironomid pupae	—	7·7	—
Chironomid adults	7	7·3	4·2
Povilla adults	2	1·6	2·1
Terrestrial insects	32	10·6	3·3
Isoptera	10	1·6	0·8
Hymenoptera	2	7·7	1·3

noted that *all* the Trichoptera in the series examined were hydroptilids, which attach their minute cases to leaves of submerged plants.

Although filamentous algae are sometimes represented, the plants eaten are mostly submerged aquatic angiosperms. *Najas* featured most often, and then species of *Hydrilla*, *Vallisneria* and *Potamogeton*. Of 360 plant-eating fishes, 85·6 per cent contained green and fresh material, and in at least 54·9 per cent of these the fragments had been bitten off the living plant.

Fish remains were found in 20·7 per cent of fishes and provided the main contents in 11·6 per cent. Corrected occurrence totals (see p. 6) showed that at least 65 per cent of the fishes eaten were cichlids, but since non-cichlids were recognized in only 6 per cent the true value for cichlids is probably far higher than 65 per cent. Nearly all the cichlids were *Haplochromis*, *Tilapia* remains having occurred in only one of the 113 piscivorous individuals examined. Fish remains were represented by detached fragments or by whole specimens. It appears that small fishes (*Haplochromis* up to about 25 mm. and *Engraulicypris* up to about 45 mm.) are ingested whole, whereas larger ones have portions bitten out of them. This suggests that *Alestes*, like *Protopterus*, may damage fishes caught in nets. Several individuals contained fish eggs and embryos.

Molluscs, which play a very small part in the diet, are mainly gastropods (*Bellamya*, *Bulinus*, *Gabbia*, *Melanoides*) and are present as shells and opercula.

It appears from Tables 25 and 26 that plants are eaten most over a soft bottom, where they provide by far the most important food, and least over a hard one—an observation consistent with the denser plant growth encountered

in sheltered regions where fine sediment accumulates. On the other hand the availability of another important food, terrestrial insects, will depend not on bottom-type, but on such factors as proximity to land, and position with regard to prevailing wind. It may therefore be concluded that plants are the preferred food of *A. jacksoni*, since it is only in those habitats where they are sparse that it feeds extensively on other foods. It is interesting to note that herbivorous tendencies are also shown by *Alestes macrophthalmus* Günther in the Malagarasi swamps (E.A.F.R.O., 1952).

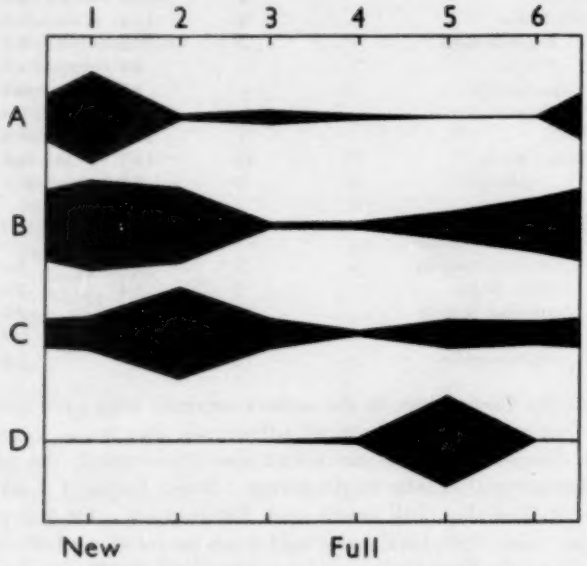


Fig. 13.—*Alestes jacksoni*. Lunar periodicity of feeding in a pelagic fish in Lake Victoria.
Abscissa : periods 1–6 in lunar month.
Ordinate : percentage occurrence (various scales) of five foods.
A. Chironomid pupae (as main contents).
B. Chironomid pupal exuviae.
C. Chironomid adults.
D. *Povilla* adults.

In only two habitats (mixed and soft) were enough fishes examined for change in food with size to be investigated. In these, there were indications that larger individuals ate more fishes (cichlids).

Conclusions

A. jacksoni has a varied diet, but feeds by preference on leaves of submerged aquatic plants which, over a soft bottom, constitute its main food. Insects, taken mainly at the surface, provide another important food, but only in regions where plants are sparse. Only a few, large insects are taken from the bottom. Fish remains comprise the only other important food, many

of these apparently being derived from fishes mutilated in nets. Its food shows that it is essentially an inhabitant of the littoral zone.

The fact that *A. jacksoni* feeds most heavily on surface insects at new and full moon would make it reasonable that gill-net (though not seine-net) catches of this species should be greatest at these two times. If this indeed proves to be so, we may expect to encounter the same phenomenon in other lakes where surface-emerging insects exhibit lunar periodicity.

ALESTES SADLERI Boulenger

Like *A. jacksoni*, this species is also found in shallow coastal waters of Lake Victoria (Greenwood, 1956 a). It is too small to be caught save by seine, rod and line, trap or explosive. Material examined from Lake Victoria consisted only of one sample, collected on a single occasion from one place. This being so, I have included here analyses of samples from Lakes Kyoga and Nabugabo, since no information otherwise exists concerning the food of this fish.

TABLE 27

Derivation of *Alestes sadleri*.

	Lake			Totals
	Victoria (HARD)	Nabugabo	Kyoga	
Numbers examined	108	9	117	234
Numbers containing food	108	9	112	229
Size-ranges (cm.)	7–9	9–10	5–9	5–10

Lake Victoria

The fishes had been feeding wholly on insects, almost all of which had been taken at the surface. These were mainly emerging adults of a small species of *Cloeon*. (It is noteworthy that the Ephemeroptera larvae eaten by three fishes were all pharate, and therefore probably also taken at the surface.) Adult Trichoptera eaten were *Pseudoleptocerus schoutedeni* and *Cheumatopsyche copiosa* ; and occasional items included Hydracarina and eggs, probably of fishes.

It cannot be deduced from this sample that the feeding habits of *A. sadleri* necessarily differ from those of *A. jacksoni* in Lake Victoria, since the fishes were obtained from over a hard bottom when an abundant supply of surface insects was present.

Lake Nabugabo

The provenance of these fishes was uncertain. Plant remains occurred in eight, chironomid pupae in three and free-living Ephemeroptera larvae in two specimens.

TABLE 28

Alestes sadleri : percentage occurrence in two lakes.

Food	Lake Victoria	Lake Kyoga
Insects	100·0	66·1
Chironomid larvae	0·9	1·8
Povilla larvae	3·7	—
Ephemeroptera : free-living larvae	2·8	—
Zygoptera larvae	0·9	—
Trichoptera larvae	0·9	—
Plants	2·8	86·7
Plants, living	—	59·0
bitten	—	50·0
Surface forms		
Chironomid pupae	75·9	6·3
Chironomid breathing organs	50·9	0·9
Chironomid adults	4·6	12·5
Ephemeroptera adults	94·4	2·7
Trichoptera pupae	7·4	—
Terrestrial insects	18·5	41·1
Hymenoptera	13·9	4·5

TABLE 29

Alestes sadleri : percentage main contents in two lakes.

Food	Lake Victoria	Lake Kyoga
Plants	—	31·3
Plants, living	—	27·7
bitten	—	25·0
Surface forms		
Insects	99·1	8·0
Chironomid pupae	10·2	1·8
Chironomid adults	1·8	1·8
Ephemeroptera adults	86·1	—
Terrestrial insects	0·9	4·5
Hymenoptera	0·9	1·8

Lake Kyoga

Three fishes were obtained in a trawl (S. H. Deathe) from an unspecified habitat. All contained plants and chironomid pupae, and two terrestrial insects (Hymenoptera and Diptera : Muscidae).

The remainder were caught on rod and line (with flour paste bait) at Budonga and Kele—probably, though not definitely, over a soft bottom. The diet (Tables 28 and 29) resembles closely that of *A. jacksoni* feeding over a soft bottom in Lake Victoria.

Fishes had been feeding mainly on submerged aquatic vegetation, including *Najas*. Of ninety-seven plant-eating fishes, 67 per cent contained green and fresh material, and in at least 84 per cent of these the fragments had been bitten off the living plant.

Insects taken at the surface included terrestrial Coleoptera, Diptera, and teneral Zygoptera (*Pseudagrion*).

Many of the specimens examined had insect remains in the intestines, and so presumably had been feeding on these previously.

Data are insufficient for changes in diet with size or habitat to be discerned. It is probable that, as in *A. jacksoni*, plants are eaten more over a soft bottom.

Conclusions

In the two habitats sampled *A. sadleri* showed feeding habits closely similar to those of *A. jacksoni*, submerged aquatic plants providing its main food in some places, and surface insects in others. It is likely, although not demonstrated, that over a soft bottom, plants would be its preferred food. The main difference between the food of the two species seems to be that *A. sadleri* eats smaller animals, and that, accordingly, it rarely if ever feeds on fishes.

DISCUSSION : CHARACIDAE

The two Lake Victoria species of *Alestes* resemble each other in being primarily herbivorous inhabitants of the littoral zone, and in obtaining much additional food from insects, taken mainly at the surface. It seems that in appropriate places both species could easily become surface scavengers, as is *A. macrolepidotus* (Cuvier & Valenciennes) at Butiaba, Lake Albert (Worthington, 1929) ; and in this connection it is interesting to note that numerous *Alestes* were attracted to crocodile carcases discharged recently in the Buvuma Channel, Lake Victoria (Garrod, personal communication). Differences between the two species in Lake Victoria appear to result from their sizes. Thus *A. jacksoni* differs from *A. sadleri* in eating larger insects, and in feeding on fishes, although it is of very slight importance in the latter respect, and is probably not the agent primarily responsible for killing most of the fishes it eats.

Ecologically, also, it may well be that size forms the main distinction between the two species, by determining their predators. As herbivorous fishes, they are valuable as primary producers of animal protein, especially since *A. jacksoni*, at any rate, is available in varied littoral habitats. Yet recorded predators are few. In Lake Victoria crocodiles eat *A. jacksoni* sparingly (Cott, 1954 ; Corbet, 1960 a), although in the Semliki River, Lake Albert and the Murchison Nile they may feed on *Alestes* more heavily (Cott, 1954), perhaps because the common species there (*A. dentex* (L.), *A. baremose* (Joannis) and *A. macrolepidotus*) are larger. It is unlikely that crocodiles in Lake Victoria feed to a significant extent on *Alestes* for this reason, since by the time crocodiles reach their fish-eating phase, they favour larger prey. *Alestes* has also been recorded as the food of the long-tailed cormorant, *Phalacrocorax africanus* (Gmelin) (Cott, 1952). Unless birds of this type are found to feed heavily on *Alestes*, it appears that in Lake Victoria there is at present no predator of suitable size or habits to exploit this valuable food. Recent work by Stoneman (1959), who has recorded the food of 246 *Lates niloticus albertianus* Worthington from Lake Albert, is relevant to this question. The main food of *Lates* averaging about 45 lb. consisted of the pelagic characids *Hydrocyon forskali* Cuvier and *Alestes*. If these records are representative, and as *Hydrocyon* is absent from Lake Victoria, it is reasonable to assume

that in Lake Victoria *Lates* of a similar size would feed very heavily on *Alestes*. This, however, should not be considered a recommendation for the introduction of *Lates* into Lake Victoria, since there are other ecological considerations which make it highly undesirable to do so (see Fryer, 1960).

CYPRINIDAE

LABEO VICTORIANUS Boulenger

This is very common in shallow regions of Lake Victoria, and also in affluent rivers (e.g. Nzoia, Kagera), where resident populations are greatly augmented by upstream migrations of breeding fishes during the rainy seasons (Whitehead, 1959). Spawning occurs in flood-water adjacent to rivers, and also in flooded margins of small affluent streams (Fryer & Whitehead, 1959).

Stomachs examined in the past (Graham, 1929 ; Worthington, 1929) all contained unidentifiable slime, and consequently the food of this fish for long remained a mystery. Recently, however, it has been shown that species of *Labeo* are specialized algal grazers : *L. cylindricus* Peters has been observed in Lake Nyasa browsing on horizontal rock surfaces (Fryer, 1959 b) and elsewhere on the backs of submerged hippopotami (see Greenwood, 1956 a). An interesting extension of this habit shown by *L. victorianus* is to feed on rotifers growing on the bodies of other fishes (Fryer, Greenwood & Trewavas, 1955).

My examination of eleven fishes from Lake Victoria confirms these observations. Of nine specimens from a mixed bottom, eight contained fine slush including diatoms resembling *Pediastrum*, *Melosira* and *Surirella*, and some fragments of plant tissue. Two fishes from hard bottoms contained fine sand grains and algal slush, and one a water-mite. It is clear that these fishes had been feeding on algae near the bottom.

Labeo victorianus is evidently a specialized and efficient feeder on epilithic and epiphytic algae. In Lake Victoria it is one of the few large fishes to utilize this source of food, a situation in marked contrast to that obtaining in Lake Nyasa, where a large and varied fish population feeds on epilithic algae (Fryer, 1959 b). *L. victorianus* is an esteemed food of natives in East Africa and is caught in large numbers by fishermen and smoked. Crocodiles have been recorded as occasional predators of adult *Labeo* in Lake Albert waters (Cott, 1954), but they do not seem to utilize them much. In Lake Victoria, *L. victorianus* constitutes a rich food supply, at present utilized principally by man.

GARRA JOHNSTONI (Boulenger)

Several specimens of this small fish were collected by E.A.F.R.O. from the Victoria Nile below the Owen Falls Dam, on occasions in 1956 when the rocks of the river bed were artificially exposed. Living under torrential conditions such as these, *G. johnstoni* would seldom if ever be caught by conventional methods, and therefore its distribution may be far wider than collections indicate.

Twelve fishes (42 to 67 mm.) from this habitat were examined, and all contained food. All were obtained before treatment of the river with DDT began in 1956. The gut contents (Table 30) show that in this habitat the

TABLE 30

Garra johnstoni : occurrence and main contents in Victoria Nile.

Food	Occurrence	Main contents
Algae and grit	11	9
Diatoms	10	—
" *Rhopaloidea* "	10	—
Filamentous algae	6	—
Lithophilic insects	8	1
Ephemeroptera larvae	8	—
Tricorythus larvae	4	1
Trichoptera larvae	3	—
Number containing food	12	12

food consists very largely of epilithic algae, but is regularly supplemented by small quantities of lithophilic insects, which are mainly Ephemeroptera larvae. The shape of its mouth (see Greenwood, 1956 a), and the presence of grit in most stomachs, show that the food is scraped from the rock surface. It may therefore be that more Ephemeroptera than Trichoptera are eaten, because the former are flatter and therefore more likely to be ingested adventitiously by a grazing feeder.

Other algae eaten were assigned to the types of *Cocconema*, *Gomphocymbela*, *Melosira*, *Oedogonium*, *Oscillatoria* and *Surirella*. One fish contained a hydropsychid larva, and another a chironomid larva.

In its feeding behaviour, *G. johnstoni* closely resembles *Labeo*, perhaps differing in eating more insects. If it occurs in Lake Victoria, it presumably inhabits exposed rocky shores.*

ENGRAULICYPRIS ARGENTEUS (Pellegrin)

As Graham has observed (1929), *E. argenteus* is a fish of riverine origin which in Lake Victoria has adopted a pelagic form and habit. In the lake shoals can often be seen moving through inshore shallows, and specimens have also

TABLE 31

Derivation of *Engraulicypris argenteus*.

	Lake Victoria			Victoria Nile	Totals
	HARD	MIXED	SOFT		
Numbers examined	102	10	6	9	127
Numbers containing food	92	10	6	7	115
Size-ranges (mm.)	12–60	48–57	31–55	42–77	12–77

been taken near the surface over deep water (Graham, 1929), thus demonstrating the truly pelagic nature of the species. *E. argenteus* has also been collected in torrential reaches of the Victoria Nile. Specimens examined were derived as in Table 31.

* Recent captures by Mr J. P. C. Greenway at Entebbe have confirmed this.

Lake Victoria

The four specimens examined by Graham (1929) contained planktonic Crustacea, including Cladocera and Copepoda.

A single sample contributes very largely to my records. This comprises eighty-three specimens (76 with food) collected while still alive at the surface during a large scale mortality of fishes at Entebbe in August 1953 (E.A.F.R.O.). They were collected over a sandy bottom. But as the food of all fishes from

TABLE 32

Engraulicypris argenteus : percentage occurrence and main contents in Lake Victoria.

Food	Occurrence	Main contents
Zooplankton	96	49
Cladocera	87	32
Copepoda	28	17
Phytoplankton	17	—
Bacillariaceae	15	—
Surface insects	6	3
Other insects	3	—

Lake Victoria for which quantitative records were kept was extremely similar, results for them have been combined in Table 32. They amply confirm Graham's observation that the food consists of zooplankton, and show that this is in fact the only important item in the diet. Little significance need be attached to the relative proportions of Cladocera and Copepoda since these probably vary from one place to another.

Although about 18 per cent of fishes contained phytoplankton (mainly diatoms), it is not certain whether or not these were eaten purposely and digested. At all events, they contribute very little by volume to the food.

Apart from zooplankton, the only food eaten to an appreciable extent is insects, which are taken from the surface. These include newly-emerged adults of chironomids and Ephemeroptera (small *Cloeon*). (One fish had been feeding on *Cloeon* in company with *Alestes sadleri*, *q.v.*) Other arthropods, represented by chironomid larvae and Hydracarina, occur so rarely as to be insignificant.

Victoria Nile

Seven fishes containing food were collected from the river bed below the Owen Falls Dam at Jinja. Crustacea (Cladocera and Copepoda) occurred in three (providing the main contents in two) ; surface insects (small Diptera) in two (2) ; and bitten plant fragments in one. Although the record of plant material may be fortuitous, it is nevertheless interesting to remark that another cyprinid, *Barbus altianalis*, apparently feeds more on plants in the Victoria Nile than in Lake Victoria.

Conclusions

E. argenteus is exceptional in Lake Victoria in being highly adapted for pelagic life, and in deriving almost all its food from zooplankton. As a small inhabitant of the open water, it forms a widely important food of the fishes

and birds which feed there. Amongst fishes the main predators of *E. argenteus* are the siluroids, *Schilbe mystus*, *Clarias mossambicus*, and *Bagrus docmac*, of which the first, itself a fish showing pelagic tendencies, is by far the most important. *Alestes jacksoni*, *Barbus altianalis* and a few other species eat *E. argenteus* occasionally, but are of little significance as predators. Water-birds which prey on *Engraulicypris* include the pied kingfisher, *Ceryle rudis* (L.), the little egret, *Egretta garzetta* (L.), the pelican *Pelecanus onocrotalus* L., the darter, *Anhinga rufa* (Lacépède & Daudin), the cormorant, *Phalacrocorax carbo* (L.) (Graham, 1929) and the long-tailed cormorant, *P. africanus* (Gmelin) (Cott, 1952).

E. argenteus is eaten regularly by man in some parts of Lake Victoria, especially shallow sandy bays in the Kavirondo Gulf, where shoals are first concentrated by floating screens of reeds, and are then scooped out in baskets.

This fish is an important and well-utilized early link in several food chains.

BARBUS ALTIANALIS RADCLIFFI Boulenger

This fish is widely distributed in shallow regions of Lake Victoria, although seldom abundant there. It is common and evident in the Victoria Nile, where fishes frequently leap clear of the water in torrential reaches. In some affluent rivers (e.g. Kagera, Nzoia) large individuals are caught in numbers as they

TABLE 33

Derivation of *Barbus altianalis radcliffi*.

	Lake Victoria			Victoria Nile	Other rivers	Totals
	HARD	MIXED	SOFT			
Numbers examined	152	209	44	53	5	463
Numbers containing food	136	146	34	46	2	364
Size-ranges (cm.)	9–64	12–54	11–90	16–78	33–57	9–90

swim upstream from the lake during the equinoctial rains. The breeding sites are unknown, although thought to be in rivers over a rock or gravel substrate (Whitehead, 1959). In specimens examined for food (Table 33) the contents of the whole gut were recorded.

Lake Victoria

Graham (1929) examined thirteen fishes containing food : ten contained molluscs only, one fishes only, and two molluscs and insect larvae. Twenty-five fishes from Lake Kyoga examined by Worthington (1929) had fed chiefly on water-weeds, although a few contained molluscs and fishes. In Lake Kivu, also, Verbeke (1957 b) has recorded that the chief food of this species is aquatic plants.

The samples analyzed here (Tables 34 and 35) show that the main food in Lake Victoria is gastropod molluscs, of which a variety of species is eaten. Gastropods occur in about 50 per cent of fishes, irrespective of feeding grounds.

TABLE 34

Barbus altianalis radcliffi : percentage occurrence in Lake Victoria.

Food	HARD	MIXED	SOFT
Insects	66·2	55·5	41
Chironomid larvae	20·6	32·2	12
Povilla larvae	11·0	8·2	3
Tricorythus larvae	6·6	—	—
Ephemeroptera : free-living larvae	16·9	8·2	3
Anisoptera larvae	8·8	8·9	9
Zygoptera larvae	0·9	0·7	—
Trichoptera larvae	22·8	16·4	18
Phanostoma	6·6	—	6
Ecnomus	5·1	6·2	—
Hydroptilidae	8·1	8·2	3
Copepoda	2·2	—	—
Ostracoda	11·0	15·8	9
Caridina	8·8	—	—
Potamon	2·9	—	—
Molluscs	54·4	58·2	62
Gastropoda	48·5	54·1	56
Melanoides	10·3	28·8	21
Bellamya	26·5	33·6	29
Pelecypoda	15·4	26·7	15
small species	14·7	24·0	12
large species	—	5·5	3
Fishes	8·8	10·3	12
Cichlidae	6·6	5·5	6
Haplochromis	2·9	3·4	6
Non-cichlids	1·5	1·4	—
Engraulicypris	0·9	1·4	—
Plants	19·1	39·7	35
Plants, living	13·2	37·0	32
bitten	5·1	14·4	24
Sand grains	5·9	0·5	2
Surface forms			
Povilla adults	11·8	2·7	3
Trichoptera adults	2·9	—	—
Terrestrial insects	4·4	2·7	—

By volume they always provide the main food, but assume greatest importance over mixed and soft bottoms. Pelecypods are relatively unimportant. *B. altianalis* evidently crushes the shells of the molluscs it eats, since they are usually represented in the gut by fragments, and only rarely by opercula or slime alone.

Other foods which are eaten to a significant extent are insects, plants, fishes and Crustacea.

The insects are most varied and important over a hard bottom, where they may almost equal molluscs in volume. *B. altianalis* obtains its insect food mainly from beneath the surface—Anisoptera larvae (mainly Libellulidae) and chironomid larvae providing the main items. Surface feeding occurs only occasionally, but may then be intense : twenty-one of the thirty-one records

TABLE 35

Barbus altianalis radcliffi : percentage main contents in Lake Victoria.

Food	HARD	MIXED	SOFT
Insects	24·3	13·0	9
Chironomid larvae	2·2	10·3	3
Povilla larvae	0·7	—	—
Tricorythus larvae	0·7	—	—
Ephemeroptera : free-living larvae	0·7	—	—
Anisoptera larvae	2·9	0·7	3
Trichoptera larvae	2·2	—	—
Phanostoma	2·2	—	—
Copepoda	0·7	—	—
Ostracoda	—	1·4	3
Caridina	8·9	—	—
Potamon	2·2	—	—
Molluscs	25·7	33·6	38
Gastropoda	18·4	22·6	32
Melanoides	1·5	5·5	15
Bellamya	4·4	2·7	12
Pelecypoda	2·2	3·4	—
small species	2·2	2·7	—
large species	—	0·7	—
Fishes	5·9	5·5	9
Cichlidae	5·1	4·1	6
Haplochromis	5·1	2·7	6
Non-cichlids	0·7	1·4	—
Engraulicypris	0·7	1·4	—
Plants	8·8	22·6	14·7
Plants, living	6·6	22·6	14·7
bitten	2·9	11·0	8·8
Surface forms			
Povilla adults	8·8	2·7	3
Terrestrial insects	0·7	—	—

are individuals which had engorged on emerging *Povilla*—all between two and five days after full moon. Terrestrial insects included an ant and Diptera. Insects taken from the bottom include larvae of *Neoperla spio* (Plecoptera) and of the Trichoptera *Pseudoleptocerus*, *Trichosetodes* and *Parasetodes*. The silken cases of *Povilla* and *Phanostoma* are ingested with the larvae.

Submerged aquatic plants are the second most important food over mixed and soft bottoms. They are eaten least over a hard bottom, a situation paralleled in *Alestes*. Of ninety-six plant-eating fishes, about 86 per cent contained green and fresh material and in at least 43 per cent of these the fragments had been bitten off the living plant. Of sixty-six cases in which plant remains were recognized, *Najas* (nr. *pectinata* (Parlatore) Magnus) occurred in about 76 per cent, and *Vallisneria* (nr. *spiralis* L.) in about 18 per cent.

Fish remains occurred in 9·8 per cent and provided the main contents in 6·0 per cent. Fishes evidently provide a regular food of minor importance to individuals more than 20 cm. long. It appears that, like *Povilla*, they may occasionally provide the sole food : one *Barbus* (44 cm.) had eaten at least

nine *Haplochromis* about 40 mm. long. Corrected totals indicate that, of the fishes eaten, no more than 85 per cent are cichlids, and that virtually all of these are *Haplochromis* ; no *Tilapia* remains were found in the series examined. Nearly all the non-cichlids consist of *Engraulicypris*. The finding of scales of *Protopterus* in one fish (32 cm.) raises the possibility of algal grazing (see p. 52), and it is interesting to note that at least sixteen fishes contained algal slush, resembling that found in the gut of *Labeo*, and including remains of diatoms and filamentous algae.

Crustacea eaten by larger fishes are mainly *Caridina*. The three fishes feeding on Copepoda were the smallest examined, being 9, 9 and 10 cm. long. They had been feeding on bottom-living insects over sand, but although *Barbus* may well breed in shallow sandy sites, these fishes are still too large to provide a useful clue to the breeding site, if any, in the lake.

Otherwise, indications of changes of food with size were provided only by the incidence of Anisoptera larvae and fishes (*Haplochromis*), which are seldom eaten by individuals less than 20 cm. long, but progressively more by larger fishes.

Victoria Nile

In a previous study of its food in the Victoria Nile (Corbet, 1958 a), *B. altianalis* was cited as an example of a fish likely to be affected least by DDT treatment, since its food consisted mainly of plants and also of fishes (*Engraulicypris*), terrestrial insects (Hymenoptera and Lepidoptera), molluscs and crabs, none of which are affected appreciably by riverine applications of the insecticide.

A synopsis of its food suggests that in the river more plants and fishes are eaten than in the lake. It should be noted, however, that several of the fishes were taken by angling with a lure, and that some of these contained bitten plant fragments. This suggests that individual fishes may alternate between plant and animal food.

Other rivers

Two fishes (33 and 39 cm.) caught while ascending the Nzoia River contained insects and plant debris respectively.

Conclusions

Although it has a very varied diet in the lake, *B. altianalis* derives most of its food from gastropod molluscs which, like *Protopterus*, it crushes with its jaws. It is when feeding over a hard bottom that *B. altianalis* approaches most closely the insectivorous habits of others in its genus ; over a soft bottom, when it eats more plants, its feeding habits more resemble those of *Alestes jacksoni*. There are indications that it may sometimes browse on algae in the manner of *Labeo*.

In the Victoria Nile its food consists more of plants and fishes, and less of molluscs. It thus seems probable that the benthic mollusc-eating habit has been accentuated since the lacustrine environment was invaded. Other species

of mollusc-eating *Barbus* are *B. bynni* (Forskål) in Lake Albert and the Murchison Nile (Worthington, 1929) and *B. eurystomus* (Keilhack) in Lake Nyasa (Worthington, 1933 ; Bertram, Borley & Trewavas, 1942 ; Fryer, 1959 b). As these are amongst the largest species of the genus, it seems possible that adoption of this habit has been made possible by the size and strength of their jaws.

The main predators of *B. altianalis* appear to be man (especially in rivers) and crocodiles (Cott, 1954), although probably neither exacts a heavy toll, except perhaps man during the seasons when fish weirs are extensively used. Consequently, *B. altianalis* is probably of little importance in the biological economy of the lake. Fryer (1959 a) has recently found it to serve as a host for the post larval stage of the mussel, *Mutela bourguignati* (Ancey).

Other species of Barbus

Greenwood (1957 b) lists seven other species of *Barbus* (all described by Boulenger) from the Lake Victoria basin. These are :

Barbus cf. *amphigramma*	*B. doggetti*
B. portali	*B. magdalenae*
B. minchini	*B. apleurogramma*
B. nummifer	

The first of these has recently been found to be *B. paludinosus* Peters (Greenwood, *in litt.*) and will subsequently be referred to by this name. All the species listed are small (less than 15 cm. long) and typically inhabit small streams connected with the lake. All are known to feed on insect larvae (E.A.F.R.O., unpublished), except *B. magdalenae* for which no records exist. I have examined material of two species only, and for the time being these records will have to suffice as an indication of the food of the remainder.

BARBUS PALUDINOSUS Peters

Six fishes (7 to 11 cm.) from the Kagera River were examined, of which two were empty. Two contained the gastropod, *Bulinus* ; two insect remains, including a mayfly larva ; two unrecognizable slush ; and one a sand grain. The gastropods were represented by entire shells. This fish apparently feeds on the bottom—on insects and molluscs.

BARBUS PORTALI Boulenger

Forty-eight fishes (3–7 cm.) were examined, of which three were empty. These fishes were collected from the Bokwe, Kasokwa and Waisoke Rivers, near Budongo Forest, Bunyoro, by Mr P. Hainsworth. An analysis of their food (Table 36) reveals that insects provide the main food, although plants are also eaten to an appreciable extent.

Insects are taken from the surface, but more often from submerged stones. The Ephemeroptera larvae were mainly *Afronurus* and *Tricorythus*, and the Trichoptera were all Hydropsychidae. One fish had eaten larvae and pupae of *Simulium medusaeforme* Pomeroy and another pupae of *S. alcocki*. The frequent occurrence of sand grains provides additional evidence of bottom-feeding. Other food included an adult beetle and a culicine larva. The

presence of slush may perhaps have resulted from algal grazing, but no other evidence exists for this. Some plant fragments showed tooth marks and had clearly been bitten off the plant.

TABLE 36

Barbus portali : percentage occurrence in Bunyoro rivers.

Food	
Insects	73
Chironomid larvae	13
Ephemeroptera : free-living larvae	24
Trichoptera larvae	11
Plants	42
Unidentifiable slush	24
Sand grains	17
Surface forms	
Terrestrial insects	22
Hymenoptera	9

Conclusions

The food of other ' small ' *Barbus* may well be similar to that of *B. portali*, a view supported by recent gut analyses of *B. minchini* and *B. apleurogramma* (Garrod, personal communication). Existing records indicate that insect larvae are the common food, and that this may be augmented with surface forms, plants, and perhaps in some cases with molluscs. Thus, although living in habitats liable to insecticidal treatment for *Simulium*-control, these species probably are sufficiently unspecialized feeders to be unaffected by removal of their preferred food.

Species of *Barbus* are very rarely found in stomachs of predatory fishes in the lake.

Siluroidea

BAGRIDAE

BAGRUS DOCMAC (Forskål)

Bagrus docmac is probably the commonest and most widespread siluroid in Lake Victoria, being found over a variety of bottoms in both deep and shallow water (Graham, 1929 ; E.A.F.R.O.). Its breeding habits are unknown, but the recent discovery of small specimens (down to 4 cm. long) feeding amongst rocks on the bed of the Victoria Nile suggests that in the lake juveniles may occur on exposed rocky shores. Fishes examined for food were derived as shown in Table 37, from which it may be noted that the smallest specimens from the lake were caught over a hard bottom. It may be assumed, until further data become available, that the description of the feeding habits of small fishes in the Victoria Nile applies also to those in the lake.

Victoria Nile

The figures in Table 38 show that the food of fishes in the Victoria Nile depends on their size. Those less than 20 cm. long feed mainly on lithophilic

TABLE 37

Derivation of *Bagrus docmac*.

	Lake Victoria			Lake Nabugabo	Victoria Nile	Other rivers	Totals
	HARD	MIXED	SOFT				
Numbers examined	607	613	169	1	41	3	1434
Numbers containing food	485	500	127	1	35	3	1151
Size-ranges (cm.)	11–87	16–94	20–99	60	4–65	11–70	4–99

insects, particularly Ephemeroptera larvae, and only to a slight extent on fishes. For individuals above 20 cm. fishes provide the main food, whereas insects are hardly eaten at all. It should be noted that this difference is related to size and not to removal of lithophilic insects by DDT during the sampling period. Although six fishes of the larger size-group were caught while the lithophilic insect fauna was reduced, their food was virtually the same as that of others caught when conditions were normal, and they have therefore been included in the sample.

TABLE 38

Bagrus docmac : occurrence and (main contents) in the Victoria Nile.

Food	Size-group in cm.	
	4–17	24–65
Insects	22 (17)	3
Chironomid larvae	11 (1)	—
Chaoborid larvae	3	—
Povilla larvae	4	—
Ephemeroptera : free-living larvae	11 (2)	1
Tricorythus larvae	18 (5)	—
Anisoptera larvae	—	1
Trichoptera larvae	10 (1)	1
Phanostoma	7 (1)	1
Hydroptilidae	1	1
Trichoptera pupae	3	—
Potamon	—	3 (2)
Gastropoda	1	—
Fishes	8 (4)	10 (8)
Cichlidae	1	6 (3)
Haplochromis	—	5 (3)
Tilapia	—	1
Non-cichlids	4	5 (3)
Engraulicypris	—	1 (1)
Number of fishes containing food	22	13

Ephemeroptera larvae eaten included *Afronurus ugandanus*, and the Anisoptera larva, found in a fish of 24 cm., was *Trithemis*. The fish containing *Tilapia* remains (of a fish of *ca* 20 cm.) was itself 65 cm. long, and its stomach also contained scales and fin-rays of *Barbus altianalis*, as well as a steel fish hook embedded in its wall.

Other rivers

One fish (11 cm.) from the Kagera River had fed entirely on Ephemeroptera larvae (*Afronurus* and *Baetis*). Two fishes (66 and 70 cm.) caught in a fish-weir in the Nzoia River contained several large non-cichlids (*Labeo*, *Barbus* and *Schilbe*) which are listed in Table 41, but these records do not necessarily indicate typical feeding habits, since large predatory fishes are known to swallow smaller ones under the unusual conditions of confinement and capture (see Kow, 1950).

Lake Victoria

Graham (1929) recorded the food of 171 *B. docmac* from Lake Victoria, and concluded that the species is typically piscivorous, but that in deeper water prawns are an important food. Worthington's examination (1929) of twenty-seven specimens from Lake Kyoga and twenty from Lake Albert confirmed the importance of fishes in the diet, and showed that insects are also eaten. A single specimen (60 cm.) examined by me from Lake Nabugabo had fed on a cichlid fish.

TABLE 39

Bagrus docmac : percentage occurrence in Lake Victoria.

Food	HARD	MIXED	SOFT
Insects	38·4	17·0	20·5
Chironomid larvae	4·1	3·8	2·4
Chaoborid larvae	2·4	1·8	2·4
Povilla larvae	15·1	1·0	3·2
Ephemeroptera : burrowing larvae	0·4	—	—
Ephemeroptera : free-living larvae	2·3	0·4	—
Anisoptera larvae	16·3	2·0	10·2
Zygoptera larvae	0·4	—	—
Trichoptera larvae	1·4	0·2	—
Ostracoda	0·4	—	—
Caridina	4·1	5·8	1·6
Potamon	1·8	—	4·0
Molluscs	5·8	2·6	8·0
Gastropoda	4·8	2·0	8·0
Pelecypoda	—	0·8	0·8
Fishes	87·5	94·6	85·8
Cichlidae	60·8	78·8	63·0
Haplochromis	52·8	63·6	48·0
Tilapia	1·2	1·8	4·7
Non-cichlids	7·6	2·4	10·4
Engraulicypris	1·0	1·6	1·6
Plants	4·7	2·0	15·2
Plants, living	0·4	0·4	3·2
" Flower-buds "	3·0	12·2	2·4
Surface forms			
Povilla adults	3·0	0·2	1·6
Ephemeroptera adults	0·2	—	—
Terrestrial insects	1·6	3·2	3·2
Isoptera	—	1·6	—
Hymenoptera	0·8	0·4	0·8

Habitat

The records presented here (Tables 39 and 40) confirm that in the lake *B. docmac* is primarily piscivorous : fishes always predominate as food, irrespective of feeding-ground. Anisoptera larvae, *Potamon* and *Caridina* may also be important, but show no consistent relationship with habitat. It appears, however, that more insects are eaten over a hard bottom. The majority of fishes eaten are cichlids of which almost all are *Haplochromis*. *Tilapia* was of negligible importance in the samples studied, and occurred in only 1·9 per cent of stomachs—a value considerably less than the 5·7 per cent recorded for non-cichlids.

TABLE 40

Bagrus docmac : percentage main contents in Lake Victoria.

Food	HARD	MIXED	SOFT
Insects	6·4	1·0	4·7
Chironomid larvae	—	0·2	—
Chaoborid larvae	0·2	—	—
Anisoptera larvae	5·6	0·4	4·7
Caridina	—	1·0	—
Potamon	1·2	—	0·8
Molluscs	0·4	—	—
Gastropoda	0·2	—	—
Fishes	54·6	68·2	53·5
Cichlidae	43·1	62·6	44·1
Haplochromis	37·7	51·0	35·4
Tilapia	0·8	0·6	1·5
Non-cichlids	4·6	0·8	5·5
Engraulicypris	1·0	0·4	1·5
" Flower-buds "	—	0·2	—
Surface forms			
Povilla adults	0·2	—	—
Terrestrial insects	0·2	0·8	—
Isoptera	—	0·6	—
Hymenoptera	0·2	—	—

Amongst *Bagrus* more than 15 cm. long, *Haplochromis*, of which at least thirty species are eaten, are seldom less than four times as important by volume as any other food. The actual occurrence of *Haplochromis* must significantly exceed the values in Tables 39 and 40 : corrected occurrence totals (see p. 6) for over 1,000 *Bagrus* show that 90·6 per cent had fed on fishes, 78·6 per cent on cichlids, and 57·1 per cent on *Haplochromis*. Since, however, little more than 5·7 per cent had fed on non-cichlids, it is evident that the true values for cichlids (and thus for *Haplochromis*) must be higher still.

Of the 1151 fishes examined, from lake and river, only seventy-four (6·4 per cent) contained non-cichlid remains. In twelve of these, only scales (of *Barbus altianalis* and *Protopterus aethiopicus*) were present. In most other cases, however, the remains indicated that the prey had been ingested whole,

and such occurrences are recorded in Table 41. It is evident that, although *Engraulicypris* is the main non-cichlid prey, considerable numbers of small *Clarias* and *Mastacembelus* are eaten over rocky bottoms in the lake. In one such habitat, for example, one *Bagrus* (37 cm.) had eaten four *Clarias* ; three *Mastacembelus victoriae* ; and three *Haplochromis*, while another (34 cm.) contained nineteen *Clarias* ; three *M. victoriae* ; two *Haplochromis* ; one cichlid ; six cichlid eggs and a *Povilla* larva. These records of small *Bagrus*, *Clarias* and *Mastacembelus* living in rocky habitats in the lake are particularly interesting in so far as they support the contention that young fishes adopt the same habit there as in the river. The records in Table 41 from *Bagrus* caught in fish-weirs have been discussed above. The only other non-cichlid known to be eaten by *Bagrus* is *Synodontis*, recorded by Graham (1929). The objects recorded in Tables 39 and 40 as ' flower-buds ' are thought to be relics of digested fishes, probably eye-lenses.

TABLE 41

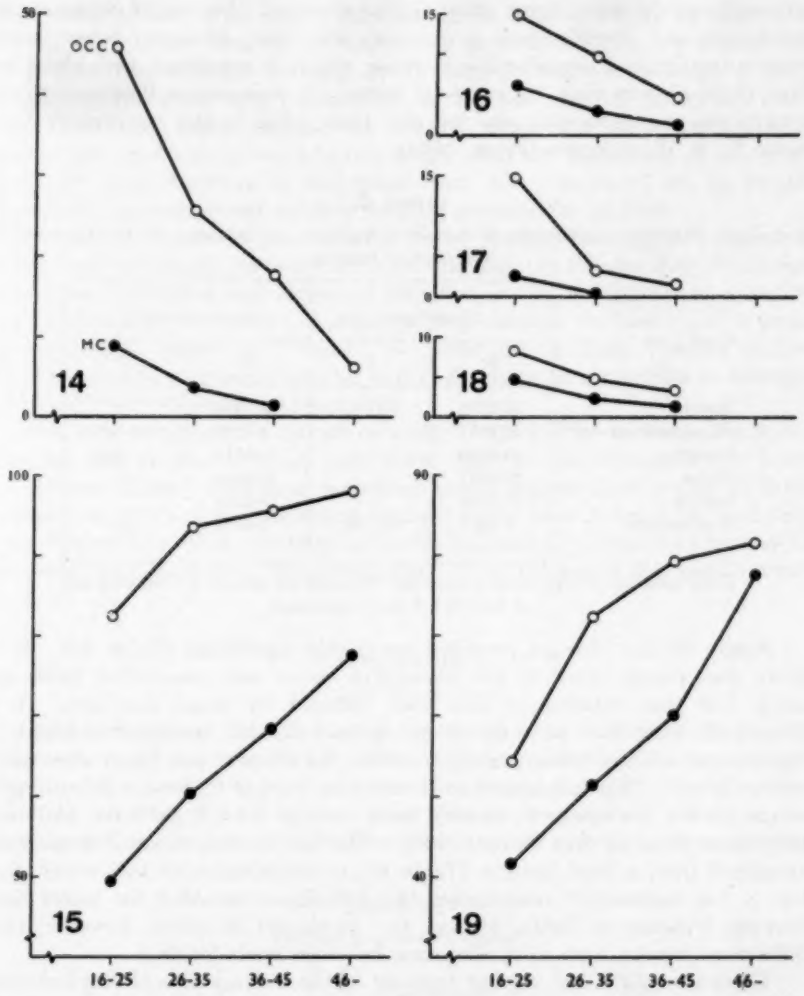
Bagrus docmac : occurrence of genera in 74 stomachs containing non-cichlid remains.

Genus of prey	No. of stomachs	Size-range of prey (mm.)	Remarks
Engraulicypris	15	unrecorded	1 in Victoria Nile.
Clarias	13	19–100	Lake : rocky bottom. 1 *C. mossambicus* ; 2 probably *C. carsoni* (1 of which from Victoria Nile).
Mastacembelus	12	35–150	Lake : rocky bottom.
Bagrus	6	85–170	Lake : rocky bottom ; 1 in Victoria Nile.
Barbus	6	90–120	1 in Victoria Nile ; 1 in fish-trap, Nzoia. Rest from lake, at least 2 being *B. altianalis*.
Alestes	2	—	Lake : fragments only.
Labeo	2	180–200	Both in fish-trap, Nzoia.
Schilbe	1	180	In fish-trap, Nzoia.
Gnathonemus	1	160	In Victoria Nile.

It is clear from Tables 39 and 40 that, although larger *Bagrus* eat a wide variety of animals other than fishes, only Anisoptera and *Povilla* larvae are eaten regularly, and of these only the former are important. The species most often represented are *Ictinogomphus ferox*, *Phyllomacromia picta*, *Trithemis annulata* and *Brachythemis leucosticta*, all of which rest on the top of sediment, or cling to rocks. Surface-feeding is uncommon, and involves occasional exploitation of mass emergences. *Povilla* adults were eaten only between three and six days after full moon. There is also a single record of a large fish in Lake Victoria having taken a duck from the surface (Pitman, 1957).

Size

The transition from an insectivorous to a piscivorous habit, occurring in the river when fishes are about 20 cm. long, has already been noted. For fishes above 15 cm. long in the lake, the occurrences of fourteen food items



Figs. 14–19.—*Bagrus docmac*. Change of food with size in Lake Victoria.
Fig. 14. Insects; Fig. 15. Fishes; Fig. 16. Anisoptera larvae; Fig. 17. *Caridina*; Fig. 18. Non-cichlids; Fig. 19. Cichlids.
Abscissa: size-groups in cm.
Ordinate: percentage occurrence (empty circles) or main contents (full circles).

were analyzed according to four size-groups of fishes from the three habitats (one hard and two mixed) for which adequate records were available. As similar trends appeared in all habitats, the data have been combined for analysis and presentation. The only changes described here (Figs. 14–19 and Table 42) are for those items which regularly provide the main contents,

although certain other items show similar changes. Larvae of chironomids, chaoborids and *Povilla* show a decrease with size, whereas 'flower-buds' show a regular and considerable increase, which is consistent with the view that these objects may be relics of fishes. A progressive decrease in the importance of insects with size has also been noted in the piscivorous *Esox lucius* L. in Windermere (Frost, 1954).

TABLE 42

B. docmac. Statistical significance of changes of food with size of fish. All X^2 values are for 3 degrees of freedom.

Food	Occurrence		Main contents	
	X^2	P	X^2	P
Insects	50·1770	·	16·7406	·
Anisoptera larvae	17·6617	·	9·7470	<·025
Caridina	45·0988	·	13·3110	<·005
Fishes	26·3927	·	18·2325	·
Cichlids	31·9273	·	16·3894	·
Non-cichlids	7·8507	<·05	5·5099	>·2

If no value for P is given, it is less than ·001, and the change of food with size is therefore highly significant.

Nearly all the changes recorded are highly significant (Table 42). It is likely that trends observed for Anisoptera larvae and non-cichlid fishes are valid, but that significance has been reduced by small numbers. It is abundantly clear that, as in the river, insects and fishes are complementary in importance, smaller fishes feeding more on the former, and larger ones more on the latter. This indicates that in the lake, young *B. docmac* inhabit sites where insects are common, namely hard bottom littoral habitats, and that they leave these as they become older. The fact that more small fishes were examined from a hard bottom (Table 37) is consistent with this conclusion, but it has necessarily accentuated the differences recorded for insect food between habitats in Tables 39 and 40. It should be noted, however, that differences remain even after allowance has been made for this.

There is a slight but regular increase in the average size of *Haplochromis* eaten by *B. docmac* as they grow larger. The mean estimated lengths of 769 *Haplochromis* eaten by *Bagrus* of the four size-groups recognized in Figs. 14–19 were 31·8, 55·7, 65·2 and 79·1 mm., respectively.

Conclusions

In the Victoria Nile, and probably also in Lake Victoria, small *B. docmac* live amongst rocks and stones and feed on the lithophilic insects there. When they exceed a length of about 20 cm. in the river they change from being insectivorous to being predominantly piscivorous. Fishes more than 15 cm. long in the lake are also predominantly piscivorous, although they continue to feed on the larger insects, in progressively decreasing amounts, until

they reach 45 cm., after which they appear to subsist wholly on fish. For *Bagrus* over 15 cm. long in the lake, even under conditions when fishes are eaten least (i.e. amongst those 15–25 cm. long feeding over a hard bottom), *Haplochromis* are still nearly four times as important by volume as any other food. Amongst larger *Bagrus*, the relative importance of *Haplochromis* is seldom less, and usually considerably more, than ten times that of any other food. It must therefore be concluded that, when above 15 cm. in length, *B. docmac* depends almost entirely on *Haplochromis* for its food.

Crocodiles occasionally eat *Bagrus* (Cott, 1954), but it appears that man is the only significant predator in Lake Victoria. It follows that *B. docmac* is of great ecological and economic importance : it is caught and eaten in large numbers by fishermen ; it relies on *Haplochromis* for food ; and it preys to a negligible degree on *Tilapia*. No other fish in Lake Victoria utilizes *Haplochromis* to so great an extent, and at the same time provides so effective a link between *Haplochromis* and man.

It is interesting to note certain ontogenetic similarities between *Mormyrus kannume* and *B. docmac* which may throw light on the colonization of lakes by riverine fishes. Evidence presented here suggests that young of both species may live and feed amongst exposed rocky sites in the lake, and only later disperse to exploit typically lacustrine habitats, *M. kannume* a bottom of fine mud, and *B. docmac* the open water. This subject is discussed further on p. 88.

SCHILBEIDAE

SCHILBE MYSTUS (L.)

Little is known of the habits of *S. mystus* in Lake Victoria since gill-net catches are small and irregular (Graham, 1929 ; E.A.F.R.O.). Large numbers may be caught during the rainy season as they ascend rivers to breed, but only about 23 per cent of such fishes contain food in the stomach. More of the fishes caught in the lake contain food (Graham : 47 per cent ; my records :

TABLE 43

Derivation of *Schilbe mystus*.

	Lake Victoria			Rivers	Totals
	HARD	MIXED	SOFT		
Numbers examined	226	104	96	123	549
Numbers containing food	110	64	36	28	238
Size-ranges (cm.)	13–31	19–34	13–30	12–33	12–34

49 per cent), but the proportion is still small compared with that of other predators (e.g. *Bagrus*, 80 per cent), and it seems that, during its most active feeding phase, *S. mystus* dwells in regions not effectively sampled by ordinary methods. Specimens examined for food were derived as shown in Table 43.

Lake Victoria

The earlier examination of ninety-one fishes from Lake Victoria (Graham, 1929) and 112 from Lake Kyoga (Worthington, 1929) showed that *S. mystus* feeds principally on *Haplochromis*, but also on prawns and insects. The present records (Tables 44 and 45) indicate that, although in the lake fishes always provide the most important food, more insects and fewer fishes (particularly cichlids) are eaten over a hard bottom. These data cannot be regarded as incisive, however, because the fishes had probably moved over a variety of substrata shortly before capture.

TABLE 44

Schilbe mystus : percentage occurrence in Lake Victoria and rivers.

Food	Lake			Rivers
	HARD	MIXED	SOFT	
Insects	60·0	36	53	93
Chironomid larvae	2·7	5	—	11
Chaoborid larvae	10·0	3	6	—
Povilla larvae	—	8	—	—
Ephemeroptera : burrowing larvae	9·1	—	—	29
Anisoptera larvae	—	5	3	—
Trichoptera larvae	—	—	—	7
Caridina	1·8	8	6	—
Fishes	46·4	89	42	4
Cichlids	13·6	69	17	—
Haplochromis	10·9	61	17	—
Non-cichlids	25·5	11	22	4
Engraulicypris	20·0	11	19	—
Plants	1·8	2	5	22
Surface forms				
Chironomid pupae	17·3	—	22	—
Chironomid adults	5·5	—	3	25
Povilla adults	1·8	—	—	—
Ephemeroptera adults	1·8	—	—	—
Trichoptera adults	0·9	—	—	—
Terrestrial insects	10·9	20	19	25
Isoptera	1·8	8	3	—
Hymenoptera	—	9	6	14

The relative importance of cichlids and non-cichlids evidently varies according to locality. In the 210 fishes from the lake, cichlids provided the main contents in about 25 per cent and non-cichlids in 16 per cent. Cichlids eaten are virtually all *Haplochromis* (no *Tilapia* were found in stomachs), recognizable remains being referable to *H.* sp. A. Greenwood in MS, *H. empodisma* Greenwood, *H.* sp. B. Greenwood in MS and *Astatoreochromis alluaudi* Pellegrin. The non-cichlids eaten consist almost entirely (at least 83 per cent) of *Engraulicypris*. Only three *Schilbe* contained remains recognizable as other non-cichlids. One contained a mormyrid scale, one fragments of *Barbus* and one (23 cm.) fragments of a *Barbus* (*neglectus*?) of about 65 mm. One contained a fish egg.

TABLE 45

Schilbe mystus : percentage main contents in Lake Victoria and rivers.

Food	Lake			Rivers
	HARD	MIXED	SOFT	
Insects	12·7	11	8	14
Ephemeroptera : burrowing larvae	2·7	—	—	—
Anisoptera larvae	—	3	—	—
Caridina	0·9	—	3	—
Fishes	33·6	70	36	—
Cichlidae	9·1	59	14	—
Haplochromis	8·2	53	14	—
Non-cichlids	20·0	8	17	—
Engraulicypris	16·4	8	14	—
Surface forms				
Chironomid pupae	0·9	—	3	—
Chironomid adults	1·8	—	3	—
Povilla adults	1·8	—	—	—
Terrestrial insects	4·5	8	3	11
Isoptera	1·8	3	—	—
Hymenoptera	—	3	—	4

Most insects eaten are taken at the surface and consist of terrestrial forms, including Coleoptera, Orthoptera, Lepidoptera and Hemiptera (Jassidae). The only aquatic stages eaten frequently are larvae of the burrowing mayfly, *Eatonica schoutedeni* and Anisoptera (*Ictinogomphus ferox* and *Brachythemis*).

Rivers

The only important food of *S. mystus* in rivers (Kagera and Nzoia) is terrestrial insects, which are mainly Hymenoptera. Fishes eaten are almost all non-cichlids.

Conclusions

In Lake Victoria *S. mystus* 13–34 cm. long are primarily piscivorous. Their main food is *Haplochromis*, although they feed much more heavily on non-cichlids (almost entirely *Engraulicypris*) than do *Bagrus* or *Clarias*. On the assumption that *Haplochromis* provides virtually all the cichlid food, corrected occurrence values indicate that, amongst fish-eating *Schilbe*, *Haplochromis* occur in about 60 per cent and non-cichlids in about 40 per cent. More than 80 per cent of the non-cichlids were *E. argenteus*.

Although insects are eaten in great variety, and occur in nearly as many stomachs as do fishes (51 per cent, compared with 59 per cent), they do not achieve one quarter the importance by volume of fish remains, or one half that of *Haplochromis*. The fact that most insects are taken at the surface of the water is consistent with the relatively great extent to which *Schilbe* feeds on *Engraulicypris*.

When ascending rivers to breed, *Schilbe* feeds little, and then almost entirely on insects taken from the surface, and to a slight extent on burrowing mayfly larvae.

S. mystus appears to have no regular predators in the lake, apart from man whose effect is probably insignificant, except perhaps during the rainy seasons when large numbers are caught in, and near the mouths of rivers. Thus, from an economic point of view, *S. mystus* is potentially valuable because it utilizes *Haplochromis* and *Engraulicypris*, but is not being extensively used, perhaps mainly because efficient means for catching it are lacking.

There is at present no large pelagic predatory fish in Lake Victoria which could provide an effective link between *Schilbe* and man. The little information available on the food of *Lates niloticus albertianus* does not favour the view that it would effectively fill this gap. Although Worthington (1929) found a siluroid (*Synodontis*) in one of twelve larger fishes which contained food, not one was recorded by Stoneman (1959) from the examination of more than 200 *Lates*. As *S. mystus* occurs in Lake Albert, it may be concluded that *Lates* would be unlikely to feed on it to a significant extent in Lake Victoria.

CLARIIDAE

CLARIAS MOSSAMBICUS Peters

Greenwood (1955 b) has studied the reproduction of *C. mossambicus* in Lake Victoria. Breeding occurs in small streams which flow into the lake for a short time after rain has fallen. While such streams persist, newly-hatched fishes remain in them and grow rapidly. It is probable that those individuals returning to the lake first do so when they are between about 15 and 25 mm. long. Subsequently, and until they are between about 15 and 20 cm. long, the young apparently have the habit of returning to a stream each time it floods. This being so, it is clear that the feeding habits of fishes from stream and lake should be considered separately.

The size-ranges given in Table 46 are extreme values and require comment. From the stream all except ten fishes were between 0·7 and 16 cm. ; the rest were breeding fishes between 55 and 87 cm., only two of which contained food. From the lake, one fish only (from a *Bagrus* stomach) was 5 cm. long, the remainder being between 24 and 90 cm.

TABLE 46

Derivation of *Clarias mossambicus*.

	Lake Victoria			Stream	Lake Nabugabo	Victoria Nile	Other rivers	Swamp	Totals
	HARD	MIXED	SOFT						
Numbers examined	111	142	138	197	1	6	18	1	615
Numbers containing food	55	91	70	93	1	5	5	1	322
Size-ranges (cm.)	5–78	27–89	26–90	0·7–87	90	10–90	52–76	81	0·7–90

Stream

Material was obtained from a small stream near Bugungu, Napoleon Gulf. This stream flowed through grassland and marginal *Echinochloa*—papyrus swamp, and has been described elsewhere (Greenwood, 1955 b). Young *C. mossambicus* there fed heavily on insects, particularly Anisoptera larvae, on Ostracoda, *Caridina* and non-cichlid fishes (Tables 47 and 48). Until they reached a size of about 3 cm., they fed on Ostracoda and aquatic insects, but not on fishes. Occurrences for Ostracoda in *Clarias* below and above 3 cm. were 32 per cent and 14 per cent respectively, and for fishes 0 per cent and 44 per cent.

The Anisoptera larvae included typical colonizers of temporary habitats, such as *Acanthagyna* (probably *villosa* Grünb.), *Pantala flavescens* F. and *Orthetrum*. Amongst surface forms taken were Hemiptera (Jassidae) and spiders. Gastropods included *Bulinus forskali* and *Biomphalaria*.

TABLE 47

Clarias mossambicus : percentage occurrence in stream and lake.

Food	Stream (fishes 0–15 cm.)	Lake (fishes 24–90 cm.)		
		HARD	MIXED	SOFT
Insects	63	40	23	50
Chironomid larvae	45	4	1	3
Chaoborid larvae	—	—	3	—
Povilla larvae	—	4	1	3
Ephemeroptera : burrowing larvae	—	9	—	—
Ephemeroptera : free-living larvae	5	2	—	3
Anisoptera larvae	12	18	3	4
Corixidae	—	6	3	—
Trichoptera larvae	—	2	—	1
Ostracoda	25	4	—	3
Caridina	3	15	7	6
Potamon	—	2	—	3
Molluscs	6	22	14	29
Gastropoda	6	22	10	24
Pelecypoda	—	—	6	7
Fishes	18	62	87	63
Cichlidae	3	42	76	49
Haplochromis	3	33	69	37
Tilapia	—	4	—	4
Non-cichlids	9	13	1	3
Engraulicypris	—	7	3	—
Plants	7	30	5	25
Slush	2	38	4	6
Clay	2	—	1	7
Surface forms				
Chironomid pupae	3	2	1	1
Chironomid adults	—	—	—	1
Povilla adults	—	2	1	11
Terrestrial insects	6	7	11	2
Isoptera	—	—	3	4
Hymenoptera	—	2	6	3

TABLE 48

Clarias mossambicus : percentage main contents* in stream and lake.

Food	Stream (fishes 0–15 cm.)	Lake (fishes 24–90 cm.)		
		HARD	MIXED	SOFT
Insects	35	23	6	24
Chironomid larvae	4	—	—	—
Anisoptera larvae	13	19	2	7
Ostracoda	9	—	—	—
Caridina	13	—	2	2
Potamon	—	—	—	5
Gastropoda	—	—	—	2
Fishes	48	77	92	71
Cichlidae	13	54	83	57
Haplochromis	13	46	76	43
Tilapia	—	4	—	5
Non-cichlids	35	15	2	—
Engraulicypris	—	15	2	—
Surface forms				
Povilla adults	—	—	—	14
Terrestrial insects	9	—	5	2
Isoptera	—	—	3	—
Hymenoptera	—	—	2	—

* In this table (only) values are given as a percentage of those fishes with main contents, because in relatively few smaller fishes does a single item occupy more than half the volume of food present. This makes a comparison possible between stream and lake.

The non-cichlid fishes, which provided the main food of fishes over 3 cm. long, comprised *Barbus* (1), *Clarias* (5), *C. mossambicus* (1) and *C. carsoni* (1). The *C. mossambicus* (*ca* 20 mm.) had been eaten by a fish of 77 mm., and the *C. carsoni* (*ca* 60 mm.) by one of 150 mm. Usually the predator was about four times the length of its prey. The only cichlid prey recognized was *Astatoreochromis alluaudi*. Two fishes had eaten tadpoles.

Lake Victoria

Fifty-five *C. mossambicus* examined by Graham (1929) had fed mainly on fishes, but also on insect larvae, molluscs, oligochaetes and Crustacea, including prawns and zooplankton. In the lake the principal food in all habitats is fishes, amongst which cichlids, particularly *Haplochromis*, predominate. Amongst *C. mossambicus* 25–90 cm. long, fish remains occurred in 72·4 per cent and provided the main contents in 51·4 per cent. Over 80 per cent of these remains could be classified as cichlids, and over 70 per cent as *Haplochromis*. The true values for these items are doubtless higher still, since non-cichlids accounted for only 6 per cent and *Tilapia* for only 3 per cent. Amongst larger individuals, *Haplochromis* are at least four times as important by volume as any other food, and fishes are nearly six times as important. At least fifteen species of *Haplochromis* have been recognized from stomachs, specimens referable to *H. sp.* A Greenwood in MS occurring most often ; this is a small species characteristic of soft bottoms (Greenwood, personal communication).

Only four *C. mossambicus* from the lake contained remains of non-cichlids other than *Engraulicypris*. Two of these (57 and 61 cm.) from a hard bottom contained *Mastacembelus* of 47 and 80 mm. ; one (43 cm.) from a soft bottom contained a *Bagrus* of 90 mm. ; and one (46 cm.) contained a fin and scale, probably of *Barbus*. Worthington (1929) has recorded *Synodontis* as prey in Lake Kyoga.

Other items of food are very varied, but consist mainly of aquatic insects, amongst which Anisoptera larvae predominate. These comprise mainly large species, such as *Ictinogomphus ferox*, *Phyllomacromia* and *Phyllogomphus*.

Substantial numbers of insects are taken from the surface ; and these include Coleoptera, Orthoptera, Hemiptera, Isoptera, adult Odonata, and emerging *Povilla* (between one and four days after full moon). Myriapods are also taken. Molluscs, represented by occupied but unbroken shells, are mainly *Gabbia humerosa* and *Sphaerium stuhlmanni*. The stomach of one fish (59 cm.) was full of planktonic Crustacea ; Graham (1929) and Greenwood (1957 b) have commented on this unusual feeding habit, and the possibility of gill-rakers being used to strain the plankton from the water. This method of feeding, however, is evidently rare in Lake Victoria. It is interesting to note, however, that, in another piscivore (*Esox lucius* L.) planktonic Crustacea form the principal food of young fishes (Frost, 1954).

Large *C. mossambicus* sometimes congregate in shallow water under cormorant nests in ambatch trees. Such fishes consume large numbers of *Haplochromis* (e.g. one of 81 cm. contained ten *Haplochromis* of 55–78 mm.) which are presumably dropped by parent birds when regurgitating at the nest. In one fish (89 cm.) was a cormorant (*Phalacrocorax* probably *carbo*) in process of hatching from an egg. Records collected by Pitman (1957) show that large *Clarias* quite frequently take a variety of small birds from the surface in this way, and that this is well known to native fishermen who by preference bait long-lines with fledglings when fishing for *Clarias*.

The catholic feeding behaviour of *C. mossambicus* is exemplified by one fish (43 cm.) from a mixed bottom which had eaten a *Haplochromis* (*ca* 40 mm.), a *Trithemis* larva, *Caridina*, newly-emerged *Povilla* adults, a gyrinid beetle (*Orectogyrus*), and leaves of *Najas*.

One fish (90 cm.) from Lake Nabugabo contained fish remains and gastropods (*Bulinus trigonus*).

Victoria Nile

A small fish of 19 cm. contained mainly Ostracoda, and some chironomid larvae. Three fishes between 10 and 11 cm. had fed mainly on lithophilic insects (*Tricorythus*, *Caenis*, *Phanostoma*, *Cheumatopsyche copiosa*, *Sphaerodema* and chironomid larvae) and Ostracoda. One of 24 cm. contained lithophilic insects and fish remains, and two large fishes (77 and 90 cm.) had eaten *Potamon* and *Povilla* adults, and *Potamon* and a *Barbus altianalis* of 50 cm.

Other rivers

The few fishes examined were in breeding condition and therefore perhaps not feeding normally. One of 65 cm. from the Kagera River contained a

mayfly (*Baetis*). Four (60–67 cm.) from the Nzoia River had eaten terrestrial insects, chironomid larvae and *Potamon*.

Conclusions

After hatching in temporary streams young *C. mossambicus* feed mainly on Ostracoda and aquatic insects until they reach a size of about 3 cm., after which they feed progressively more on fishes. A small sample from torrential reaches of the Victoria Nile indicates that, despite the different environment, the same ontogenetic changes in trophic behaviour occur in rivers also.

C. mossambicus has, when adult, very catholic feeding habits. Recorded food includes such diverse organisms as zooplankton, molluscs, termites and young birds, and there are in fact few items of potential food which have not at some time been found in its stomach. Despite its great adaptability, however, the food of adult fishes in both lake and river consists principally of fishes, amongst which *Haplochromis* predominate. *C. mossambicus* resembles *Bagrus docmac* in deriving most of its food from *Haplochromis* and the larger aquatic insects, but differs from it in augmenting this diet with a wider range of other foods. It also feeds slightly more (2·3 per cent) on *Tilapia*, but nevertheless cannot be considered an important predator of this genus.

Small *C. mossambicus* in streams are eaten by larger ones, and also by large larvae of the dragonfly, *Acanthagyna*, which the fishes themselves later utilize as prey. Rapid growth in such habitats is clearly of adaptive value, as it enables the species to pass quickly through a vulnerable size-range in a habitat liable to desiccation.

Small fishes in the lake may be eaten occasionally by *Bagrus docmac* and *Marcusenius nigricans* (*q.v.*), and large ones by crocodiles (see Hippel, 1946 ; Cott, 1954) but man is probably the main predator. Catches in gill-nets are small, but large numbers of breeding fishes may be caught locally when they ascend streams during the rainy seasons.

CLARIAS CARSONI Boulenger

Five of the six fishes examined contained food. Three (3, 6 and 11 cm.) from the Victoria Nile contained chironomid, *Povilla* and *Phanostoma* larvae, and terrestrial insects. Two (5 and 11 cm.) from the Agoye River, West Nile, had fed on chironomid, Ephemeroptera and Zygoptera larvae, and on adult Hymenoptera. These results conform with Worthington's observations (1932 b) on the food of thirty-five specimens in Lake Bunyoni, where this introduced fish is of economic importance. These fishes had fed on a variety of benthic animals, including insects (mainly), Crustacea, frogs and worms, but had also taken insects from the surface. Greenwood (1957 b) records fishes as prey of larger individuals. Apparently *C. carsoni* feeds mainly on moderate-sized arthropods, most, but not all of which are taken from below the surface.

In Lake Bunyoni Worthington (1932 b) recorded the otter, *Lutra maculicollis*, as a predator of *C. carsoni*.

CLARIAS ALLUAUDI Boulenger (group)

Of the three species at present referable to this group, *C. eupogon* Norman has recently been placed in the genus *Xenoclarias* (Greenwood, 1959 b) and

C. alluaudi and *C. werneri* are considered to be synonymous (Greenwood, 1957 b). The specimens described here were assigned to *C. werneri*.

Lake Victoria

Material was obtained from a floating marginal swamp of semi-aquatic grass and papyrus at Kirinya, near Jinja. In this swamp small *Protopterus* (*q.v.*) were also found.

Of twenty-two fishes examined, sixteen (29–180 mm.) contained food. Insects predominated (occurring in twelve stomachs) and comprised larval and adult aquatic Coleoptera (7), terrestrial insects (4), chironomid larvae (3), and larvae of *Povilla*, culicines and hydroptilids (1 each). Other food included Ostracoda (4), gastropods (3), plants (3) and Copepoda and Hydracarina (1 each). One fish (85 mm.) contained a cocoon of newly-hatched spiders (Lycosidae). The Ostracoda and Copepoda occurred in the smaller fishes.

Thus *C. alluaudi* resembles young *Protopterus aethiopicus* in the same habitat in feeding mainly on aquatic Coleoptera, and differs in that its prey comprises smaller organisms : Ostracoda are eaten, whereas Anisoptera larvae are not.

Victoria Nile

Five fishes, of which three (46, 72 and 88 mm.) contained food, were examined. These were obtained while the lithophilic insect fauna was severely affected by DDT, and the results cannot therefore be considered typical. However, the fact that at this time the fishes contained larvae of chironomids, other Diptera and a resistant species of *Caenis*, Copepoda and some fresh plant material suggests that the feeding habits there may closely resemble those of *Clariallabes petricola* (*q.v.*).

XENOCLARIAS EUPOGON (Norman)

Previously known as *Clarias eupogon* Norman, this species is represented by a single specimen, collected from deeper water in the Rusinga Channel (see Greenwood, 1959 b). Nothing is known of its food.

XENOCLARIAS HOLOBRANCHUS Greenwood

This small cat-fish is known from three specimens trawled in 120 feet of water near Ukerewe Island, Lake Victoria. Stomachs of two contained larval and pupal Diptera and small quantities of bottom debris (Greenwood, 1959 b).

CLARIALLABES PETRICOLA Greenwood

Until very recently, this small species was known only from the Victoria Nile where it was first collected in 1956 (Greenwood, 1956 c). A detailed account of its feeding habits and the effects upon them of DDT treatment has been given elsewhere (Corbet, 1958 a). This study was based on the examination of 299 specimens, and showed that normally the main food is lithophilic insects (occurrence 90 per cent ; main contents 47 per cent), amongst which larvae of *Tricorythus* predominate (67 per cent ; 26 per cent). In addition,

very small quantities of Ostracoda, molluscs, Hydracarina and terrestrial insects are eaten.

Although apparently a specialized feeder on lithophilic insects, this species showed greater adaptability than any other when DDT treatment removed this source of food. It rapidly changed its habits so as to exploit foods which remained, such as living plants, chironomid and tipulid larvae, pelecypods and Copepoda. As the effects of DDT wore off, its feeding habits gradually returned to normal, until a year later its diet was the same as it had been before.

Such plasticity of trophic behaviour in a changing environment shows that food *per se* is unlikely to provide a serious ecological barrier to the dispersal of such fishes, and it also emphasizes the importance of making allowance for habitat when recording the feeding habits of fishes. At different times during this investigation, the main food of *C. petricola* would have been described as lithophilic insects, plants and Copepoda, respectively.

MOCHOCIDAE

SYNODONTIS VICTORIAE Boulenger

Although found sparingly in shallow water, *S. victoriae* is apparently commoner in water more than 13 m. deep (Graham, 1929 ; E.A.F.R.O.). Specimens examined for food were derived as shown in Table 49.

TABLE 49

Derivation of *Synodontis victoriae*.

	Lake Victoria			Rivers	Totals
	HARD	MIXED	SOFT		
Numbers examined	39	2	194	39	274
Numbers containing food	25	2	174	34	235
Size-ranges (cm.)	9–23	10–16	8–19	9–19	8–23

Lake Victoria

The main food of *S. victoriae* in Lake Victoria is molluscs and insects. The sample from a hard bottom (Tables 50 and 51) is small, but nevertheless these fishes had apparently fed more on insects and less on molluscs than those from soft bottom habitats. As it appears that *S. victoriae* is found more often over a soft bottom (see also Graham, 1929), it is probably true to say that molluscs are its main food in the lake. Over hard and soft bottoms molluscs occur in 87 to 88 per cent of fishes, and over a soft bottom provide the main contents in 49 per cent, being more than nine times as important by volume as any other food.

Amongst the molluscs eaten, gastropods are about ten times as important as pelecypods, and are usually represented in stomachs by flesh and opercula without shells. Shells, if present, are not crushed. *Melanoides tuberculata* and species of *Bellamya* provide the main food (Table 52).

The *Caelatura* eaten (young specimens of *C. hauttecoeuri* and *C. monceti*) were only slightly larger than *Sphaerium stuhlmanni*, which comprised 95 per cent of the small pelecypods. Pelecypod valves were not crushed, and sometimes *Corbicula* and *Byssanodonta* were found closed and apparently undamaged in the intestine. One fish (18 cm.) from a mixed bottom contained about 100 *Sphaerium*.

TABLE 50

Synodontis victoriae : percentage occurrence in lake and river.

Food	Lake		Rivers
	HARD	SOFT	
Insects	76	62·1	97
Chironomid larvae	68	43·1	35
Chaoborid larvae	—	1·7	—
Povilla larvae	20	2·3	9
Ephemeroptera : burrowing larvae	28	—	24
Ephemeroptera : free-living larvae	40	1·7	24
Anisoptera larvae	—	9·2	—
Zygoptera larvae	—	0·6	3
Trichoptera larvae	32	4·6	32
Ecnomus	16	—	—
Oligochaeta : *Alma*	4	3·4	24
Copepoda	—	13·8	—
Ostracoda	28	10·9	6
Caridina	8	0·6	3
Hydracarina	4	8·0	3
Molluscs	88	87·4	27
Gastropoda	80	85·6	9
Melanoides	36	75·3	6
Bellamya	44	36·8	6
Pelecypoda	28	20·7	24
small species	28	19·5	21
large species	—	2·9	—
Fishes	12	5·7	3
Cichlidae	—	0·6	3
Non-cichlids	—	1·1	—
Engraulicypris	—	1·1	—
Bryozoa	—	30·4	13
Surface forms			
Povilla adults	4	—	—
Ephemeroptera adults	—	—	9
Terrestrial insects	—	8·0	35
Hymenoptera	—	4·0	15

Insects eaten most were chironomid larvae. Burrowing Ephemeroptera included *Eatonica schoutedeni*, and Odonata larvae, *Ictinogomphus ferox*, *Phyllomacromia*, *Brachythemis* and *Pseudagrion*. *Povilla* adults were taken five days after full moon ; other surface forms included a spider.

Over a soft bottom Copepoda and Ostracoda are eaten more by smaller individuals. Fragments which were probably lithophilic Bryozoa were found in about 30 per cent of stomachs.

TABLE 51

Synodontis victoriae : main contents in lake and river.

Food	Lake		River
	HARD	SOFT	
Insects	32	5·2	24
Chironomid larvae	12	2·9	6
Povilla larvae	12	—	3
Ephemeroptera : burrowing larvae	4	—	6
Anisoptera larvae	—	1·1	—
Trichoptera larvae	4	—	—
Oligochaeta : *Alma*	—	—	15
Ostracoda	4	1·1	—
Molluscs	24	49·4	12
Gastropoda	12	41·4	3
Melanoides	4	25·9	—
Bellamya	—	2·3	—
Pelecypoda	12	4·6	9
small species	12	3·4	9
Fishes	4	1·7	—
Non-cichlids	—	1·1	—
Engraulicypris	—	1·1	—
Surface forms			
Ephemeroptera adults	—	—	6
Terrestrial insects	—	0·6	3
Hymenoptera	—	—	3

TABLE 52

Synodontis victoriae : percentage occurrence of mollusc genera.

	Lake	River
Gastropoda		
Melanoides	70·1	6
Bellamya	37·8	6
Bulinus	3·0	—
Gabbia	1·5	—
Biomphalaria	1·0	—
Pelecypoda—small		
Sphaerium	20·4	—
Corbicula	1·0	6
Byssanodonta	—	13
Pisidium	—	3
Pelecypoda—large		
Caelatura	3·0	—

Fishes are eaten to a minor extent, and occurred in 6·5 per cent of the 201 specimens from the lake. Non-cichlids (*Engraulicypris*) were recorded from 1·0 per cent, and cichlids from 0·5 per cent.

Graham's (1929) examination of eighty-one stomachs (probably of *S. victoriae*) produced results significantly different from mine, and led to the conclusion that this species feeds principally on insects (chiefly larval and adult chironomids), and that its food is virtually the same as that of *Mormyrus*

kannume. A feature of Graham's sample was that many fishes had been feeding at the surface on newly-emerged chironomids and Ephemeroptera : it is possible therefore that they had been exploiting a mass emergence (apparently a large proportion of the fishes was caught on one day) which would have temporarily increased the apparent importance of insects in the diet. Worthington (1929) found molluscs in three fishes from Lake Kyoga.

Rivers

The fishes examined came from the Sondu (19), Kagera (16), and Nzoia (4) Rivers. Their food (Tables 50 and 51) resembles that of fishes over a hard bottom in the lake in so far as insects and molluscs constitute the main food, but more surface forms are taken, and pelecypods (Table 52) are more important than gastropods. Swamp-worms (*Alma* sp.) are also an important food.

Burrowing Ephemeroptera included *Ephoron* (probably *savignyi*), and the terrestrial insects, Coleoptera and Hemiptera-Homoptera. Other items included Conchostraca and Simuliidae. In the Sondu River three fishes (13, 13 and 15 cm.) contained larvae and pupae of *Simulium*.

As in the lake a considerable amount of surface feeding takes place.

Conclusions

S. victoriae is of interest in being the only siluroid, and one of the few fishes in the lake, to feed heavily on small molluscs. Amongst non-cichlids, only *Protopterus aethiopicus* and *Barbus altianalis* have similar feeding habits. *S. victoriae*, however, is able to extract the flesh of gastropods without crushing the shell. It also feeds to a much greater extent on chironomid larvae than either of these species, and in rivers it is unusual in feeding on swamp-worms.

Synodontis appear to be a frequent food of crocodiles in Lake Albert but not in Lake Victoria (Cott, 1954) where *Clarias* (Worthington, 1929), *Protopterus* (*q.v.*), and the long-tailed cormorant (*Phalacrocorax africanus*) (Cott, 1952) are apparently the only predators which have been recorded. *S. victoriae* is of local importance to fishermen in Lake Victoria at certain times of year.

SYNODONTIS AFRO-FISCHERI Hilgendorf

This species is seldom caught, but appears to be commoner in rivers than in the lake. Specimens examined were derived as shown in Table 53.

TABLE 53

Derivation of *Synodontis afro-fischeri*.

	Lake Victoria		Victoria Nile	Other rivers	Totals
	HARD	MIXED			
Numbers examined	8	7	2	16	33
Numbers containing food	7	5	2	10	24
Size-ranges (cm.)	13–15	15–20	9–11	7–13	7–20

Despite the small numbers examined, the feeding habits in lake and river (Tables 54 and 55) can be recognized as broadly similar, but show approximately the same differences as were noticed between the habitats in *S. victoriae*, which has a similar diet.

TABLE 54

Synodontis afro-fischeri : percentage occurrence in lake and river.

Food	Lake	River
Insects	100	83
Chironomid larvae	50	33
Chaoborid larvae	17	—
Povilla larvae	50	8
Ephemeroptera : burrowing larvae	—	8
Ephemeroptera : free-living larvae	—	8
Corixidae	17	—
Trichoptera larvae	25	17
Ecnomus	17	—
Hydroptilidae	8	8
Hydracarina	8	—
Oligochaeta	—	8
Ostracoda	25	—
Molluscs	50	17
Gastropoda	42	17
Plants	20	55
Surface forms		
Chironomid adults	—	8
Terrestrial insects	8	25
Hymenoptera	—	17

TABLE 55

Synodontis afro-fischeri : percentage main contents in lake and river.

Food	Lake	River
Insects	42	33
Chironomid larvae	17	8
Chironomid pupae	—	8
Povilla larvae	25	—
Simuliid larvae	—	8
Molluscs	8	8
Gastropoda	8	8
Plants	8	8
Surface forms		
Arthropoda (Isopoda)	—	8
Chironomid adults	—	8

S. afro-fischeri appears to feed less on molluscs than does *S. victoriae* and more on insects, amongst which *Povilla* and chironomid larvae predominate. In rivers (Kagera, Sondu, Nzoia, Victoria Nile) it is possible that more insects are taken from the surface, as was noted also in *S. victoriae*. It is interesting to note that eight of the fishes from rivers were taken on lines baited with *Alma*, and this also may indicate a food preference similar to that shown by *S. victoriae* in rivers. The presence of *Simulium* larvae shows that lithophilic

insects may sometimes be eaten. Gastropods included *Bulinus*, *Bellamya*, *Biomphalaria* and *Gyraulus*.

Conclusions

The diet of *S. afro-fischeri* is probably similar in scope to that of *S. victoriae*, but differs in comprising fewer molluscs. It is clearly a less specialized mollusc-eater, since it ingests the entire animals without crushing the shells. As a rare and generalized feeder in lake and river its ecological significance is probably slight.

It is caught on baited hooks by fishermen in upper reaches of rivers, but is usually discarded when taken in gill-nets in the lake. Records of predators other than man do not distinguish between this species and *S. victoriae* (*q.v.*).

AMPHILIIDAE

AMPHILIUS JACKSONI Boulenger

Although this rare stream-living fish has not yet been recorded from the Lake Victoria catchment area, it may well occur there since it has been collected from the Lwakaka River which flows into Lake Kioga but passes near the dividing water shed. No previous records exist of its food.

Four specimens (63–117 mm.) were examined. They were collected by Mr P. Hainsworth from the Aduka and Agoye Rivers (West Nile), and from the Lwakaka River (Uganda–Kenya border).

In all fishes the entire food was lithophilic insects, including Ephemeroptera (*Afronurus* and *Baetidae*), and Trichoptera (Hydropsychidae).

In the Belgian Congo, *Amphilius* spp. are regarded as typically inhabitants of the upper reaches of streams and rivers (Marlier, 1954).

DISCUSSION : SILUROIDEA

The siluroid fishes of Lake Victoria (listed in Fig. 20) do not comprise so homogeneous a group as the Mormyridae, but possess enough features in common to justify being treated together.

The food of this group, and of some of its members, is extremely varied, and in general consists of insects, crustaceans, molluscs and fishes, usually swallowed whole, and taken from all strata in the aquatic environment. The widely-adaptable feeding habits of the Clariidae are well known (see Pitman, 1957), and the recent opportunity to study the diet of *Clariallabes petricola* in a rapidly changing environment has provided the *experimentum crucis* to demonstrate how truly facultative some members of this family can be.

Superimposed upon this euryphagy, however, are certain patterns of potential specialization which—as in the Mormyridae—are revealed more clearly by a volumetric method of food assessment. The food preferences of the group are expressed on this basis in Fig. 20, in which the species have been arranged in series, so that the most piscivorous is at the top, and the most insectivorous at the bottom. It happens that these two attributes are complementary, and that therefore the series is conformable from both points of view. That such a classification is meaningful is further suggested by the

fact that the species are thereby also arranged approximately according to their size and habitat. This, in Fig. 20, the smallest, most insectivorous, riverine species are below, and the largest, most piscivorous, lacustrine ones are above.

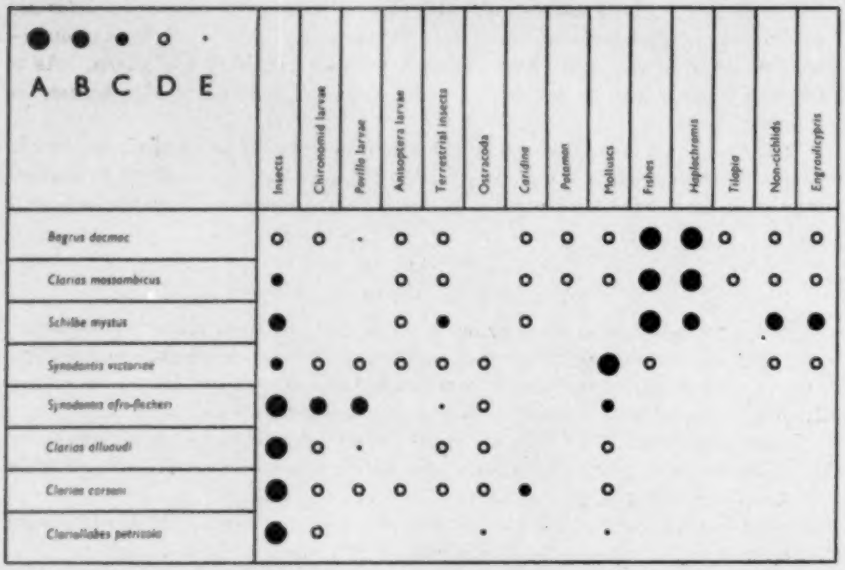


Fig. 20.—Siluroidea. Food preferences as shown by the five grades of incidence defined in Fig. 12 (p. 43). Data are from Lake Victoria except for *Clarias carsoni* (Lakes Victoria and Bunyoni (Worthington, 1932 b)) and *Clariallabes petricola* (Victoria Nile). Species are arranged so that the most piscivorous is at the top, and the most insectivorous at the bottom.

When it is recalled that, in the Lake Victoria basin, the lacustrine environment has only recently been established (see Worthington, 1937, 1954), the correlation of these three attributes leads to the conclusion that the only riverine siluroids likely to colonize the open waters of a lake would be those which were large as adults, and which consequently had left the river bed and become piscivorous. The ontogeny of *Bagrus docmac* illustrates this point : the smallest fishes feed on lithophilic insects in the river bed, whereas larger individuals feed progressively more on fishes, and are associated less with the bottom. By the same token, species which are small as adults, possibly as the result of neotenic specialization (e.g. *Clariallabes petricola* (see Greenwood, 1956 c)), will be the least likely to become lacustrine piscivores.

Here it should be remarked that, because they include the only extensively piscivorous non-cichlids in the lake, the Siluroidea should not be thought of as a primarily piscivorous group. Rather does it seem that this habit has developed only in three species which, by virtue of their size and relative freedom from benthic specialization, have been able to colonize the open waters of a lake.

As is to be expected from previous work (e.g. Allen, 1935), piscivores show the lowest proportion of stomachs containing food (Table 59), and it may therefore be assumed that they feed less frequently. A corresponding trend can not, however, be discerned amongst small and large individuals of a single species (*Bagrus docmac*) within the piscivorous size-range.

Ontogenetic changes observed in the food of *Bagrus docmac*, both in river and lake, have provided evidence for assuming that in the lake small *Bagrus* live and feed on rocky shores, and probably breed nearby. If in the lake *B. docmac* is able to breed successfully on rocky shores, then it must be regarded as the siluroid best adapted to a lacustrine life, since, although still a fairly common migrant to rivers (Whitehead, 1959), it is evidently no longer dependent on anadromesis for the maintenance of the lake population. It is interesting to note that Marlier (1953) regards this species as " plus lacustre que fluviatile " in Lake Tanganyika and the Ruzizi basin. These observations are consistent with both *B. docmac* and *Mormyrus kannume* being the most successful and lacustrine members of their respective groups. If both species are found to breed on rocky shores, it will augur well for their future exploitation, since this environment is among those most immune from predation and interference. *Schilbe mystus* and *Clarias mossambicus*, on the contrary, suffer heavy reduction in fish-traps and drift-nets while ascending rivers and streams to breed.

This study has shown the larger siluroids (especially *B. docmac*) to be of great potential value to man, since they prey to a negligible extent on *Tilapia*, yet feed heavily on *Haplochromis* and *Engraulicypris*.

CYPRINODONTIDAE

APLOCHEILICTHYS PUMILUS (Boulenger)

This small fish inhabits marginal vegetation in lakes and streams (see Greenwood, 1957 c). Specimens examined were derived mainly from habitats outside Lake Victoria (Table 56). The swamp was near Iganga, in the Lake

TABLE 56

Derivation of *Aplocheilichthys pumilus*.

	Lake Victoria	Swamp	Dam	Victoria Nile	Totals
Numbers examined	1	14	23	2	40
Numbers containing food	1	12	23	2	38
Size-ranges (mm.)	34	20–32	21–34	26–33	20–34

Kyoga catchment area (material collected by Dr G. S. Carter) ; and the dam was at Eldama Ravine in the Kenya Highlands. Results for swamp and dam have been combined in Table 57, since fishes came from thick marginal vegetation in both cases.

The fish from Lake Victoria came from a drainage ditch in marginal swamp at Kirinya, near Jinja, and contained nothing but small adult Diptera.

TABLE 57

Aplocheilichthys pumilus : occurrence in swamp and dam.

Insects		18
Hydracarina		13
Slush		12
Crustacea		3
Algae		2
Number feeding :	below surface	17
	at surface	15
	below and at surface	7
Number containing food		35

It is clear from the results (Table 57) that in swamp and dam *A. pumilus* had fed mainly on small insects taken below and at the surface. In this analysis it has been assumed that the Hydracarina were caught *below* the surface, but it is also possible that they could have been taken *at* the surface. Had this been so, the number of fishes feeding below the surface would have been eleven instead of seventeen. Thus there remains the possibility that *A. pumilus* obtains most of its food from the surface itself.

Surface forms eaten were principally Diptera (Nematocera), and also small Coleoptera, Ephemeroptera, Thysanoptera and a spider. Insects taken below the surface were chironomid and Ephemeroptera larvae and Corixidae. The Crustacea included Copepoda, Cladocera and Ostracoda. The inclusion of zooplankton in the diet is interesting in view of the plankton-feeding specialization exhibited by *A. pelagicus* (Worthington) in Lake Albert (Worthington, 1932 a).

The two fishes from the Victoria Nile (below the Owen Falls) contained larvae of chironomids, Ephemeroptera and Trichoptera (*Ecnomus*), and pupae of chironomids and Trichoptera (probably Hydroptilidae). They had thus fed mainly below, but also possibly at, the surface.

A. pumilus is an unspecialized feeder on small arthropods. By living amongst marginal vegetation it doubtless escapes the notice of several predators of a size to exploit it. Specimens have been found in stomachs of the darter, *Anhinga rufa* (Cott, 1952), and of the swamp-living mormyrid, *Mormyrus macrocephalus*.

The food of *A. eduardensis* (David and Poll), which has recently been found in Lake Victoria (E.A.F.R.O., unpublished) is unknown, although probably similar to that of *A. pumilus*. An allied species, *A. loati* Boulenger, occurs in surface shoals among swamp vegetation of the White Nile, where it may feed on larvae of *Anopheles* and *Culex* (Lewis, 1949).

Cynopanchax bukobanus (Ahl) is known only from Bukoba, Lake Victoria. Its food is unknown.

ANABANTIDAE

CTENOPOMA MURIEI (Boulenger)

This species lives in streams and swamps, and in marginal vegetation of Lakes Victoria and Kyoga (Greenwood, 1957 c).

Three specimens only have been examined. One (67 mm.) from marginal grass near the mouth of the Kagera River contained terrestrial insects (Hymenoptera and Orthoptera : Acridiidae). Two (53 and 56 mm.) from a flood-water pool in the Lugari River, Kenya (collected by Mr P. J. P. Whitehead) had eaten larvae of chironomids, Ephemeroptera (Baetidae) and Anisoptera (Libellulidae), and a small terrestrial insect (probably Coleoptera). Greenwood (*loc. cit.*) records Crustacea also as food.

The diet of *C. muriei* apparently resembles that of *Aplocheilichthys pumilus*.

MASTACEMBELIDAE

MASTACEMBELUS VICTORIAE Boulenger

M. victoriae is seldom caught in Lake Victoria, but is common amongst stones on the bed of the Victoria Nile below Owen Falls (see Table 58).

TABLE 58

Derivation of *Mastacembelus victoriae*.

	Lake Victoria		Victoria Nile	Other rivers	Totals
	HARD	Swamp			
Numbers examined	1	2	227	1	231
Numbers containing food	1	1	194	1	197
Size-ranges (cm.)	14	18–19	4–23	26	4–26

Lake Victoria

The single fish examined from a hard bottom came from the stomach of a *Bagrus docmac*. It contained only pharate *Povilla* larvae (at two days after full moon). The fish from marginal swamp had apparently been feeding on swamp-worms (*Alma*) and possibly on *Povilla* larvae. It is interesting to note that *Mastacembelus shiranus* Günther in Lake Nyasa can be caught on a bait of worms (Fryer, 1959 b).

Victoria Nile

A detailed account has already been given (Corbet, 1958 a) of the feeding habits of *M. victoriae* in the Victoria Nile, and of the way in which these were affected by DDT. In this habitat *M. victoriae* is a very specialized feeder, and depends almost entirely on lithophilic insects for its food (occurrence 97 per cent ; main contents 80 per cent). Amongst these, larvae of *Tricorythus* (78 per cent ; 35 per cent) and Hydropsychidae (51 per cent ; 10 per cent) predominate. In addition, very small quantities of chironomid and *Neoperla* larvae, Ostracoda, molluscs, fish eggs, *Potamon* and *Hirudinea* are eaten. It

is clear that virtually all feeding takes place amongst the stones of the river bed. Therefore in its habits and food, it is almost identical to *M. shiranus* in Lake Nyasa (Fryer, 1959 b), and presumably to other members of the genus elsewhere.

When the lithophilic insect fauna was removed from the Victoria Nile by DDT, *M. victoriae* was severely affected, and a significant number must have died of starvation or left the area. The few remaining fishes which had fed contained unusual foods such as Hirudinea and small fishes (post-larval *Haplochromis*). Thus, unlike *Clariallabes petricola*, which usually has similar feeding habits, *M. victoriae* must be regarded as a highly specialized feeder on lithophilic insects. This being so, it can be assumed that in Lake Victoria it inhabits rocky shores, where it may well be found to be common. Fryer (1959 b) reports that, although seldom collected otherwise, *M. shiranus* used to be caught in large numbers amongst rocks during fish poisoning operations. In this connection it is noteworthy that one of the fishes examined from Lake Victoria came from the stomach of a *Bagrus* caught over a rocky shore. In such a habitat, *M. victoriae* can have few predators, and the only records known to me are of the *Bagrus* mentioned in Table 41.

GENERAL DISCUSSION

It has become increasingly evident that the ecological significance of the feeding habits of the non-cichlid fishes cannot be discussed fruitfully except against the evolutionary background of the species concerned. The feeding habits themselves do, of course, provide some evidence for this background, principally through ontogenetic changes which can be observed, but it appears to be generally true that flexibility and adaptability of food habits are the rule in freshwater fish populations (see Larkin, 1956), and that, this being so, their evolutionary background should be deduced from less facultative characteristics, amongst which breeding behaviour, being highly specialized, is probably one of the most reliable.

An important respect in which non-cichlids differ from cichlids in Lake Tanganyika—a lake of much greater antiquity than Lake Victoria—is that they feature a higher proportion of "fluviatile species", that is fishes which are known or assumed to breed only in rivers (Poll, 1956). If, as has been assumed, lacustrine fishes evolved from riverine ancestors, then it appears that non-cichlid fishes have not progressed so far in this direction as have cichlids, and therefore may be expected still to exhibit some of the earlier stages in the process.

Before considering the successive stages by which a riverine fish can become lacustrine, it should be emphasized that the remarks which follow apply only to those species whose breeding sites in rivers do not have counterparts in lakes—that is, species for which a *definite change* of breeding behaviour is demanded if they are to breed in lakes. Thus, species such as *Protopterus aethiopicus* which breed in marginal swamp (see Greenwood, 1958) can presumably do so as well in large rivers as in lakes. Also *Engraulicypris argenteus*, which appears to lay floating eggs (Graham, 1929), would presumably find suitable sites in both habitats. Two other species which must be excluded

from the immediate discussion are *Clarias mossambicus* and *Labeo victorianus*, both of which are known to breed in small streams entering the lake after rain (Greenwood, 1955 b ; Fryer & Whitehead, 1959). These fishes exhibit a specialization which may well have arisen in rivers (larval *Clarias* have been encountered in flood pools near the Kagera River by Carpenter (1925)), and so places them in the same category as *P. aethiopicus* and *E. argenteus*, as fishes which require no modification in their behaviour to breed in lakes as well as rivers.

With these reservations in mind, we may recognize four hypothetical stages in the colonization of lakes from rivers.

(1) Feeding and breeding only in rivers.
(2) Feeding in lakes and rivers ; breeding only in rivers.
(3) Feeding and breeding in lakes and rivers.
(4) Breeding in lakes only ; feeding in lakes (and perhaps by chance in rivers near their mouths).

Progression through these stages may be expected to occur when rivers flow into a lake, particularly when, as in Lake Victoria, a regular outflow has prevented a salinity difference developing between rivers and lake (*cf.* Lake Tanganyika (Beauchamp, 1946)).

The fact that in Lakes Victoria (Whitehead, 1959) and Tanganyika (Poll, 1956) certain species of fish move from the lake to rivers to breed, indicates that for species in stage 2 of this scheme the lake is only a feeding ground, though presumably worth entering for this purpose. It is likely that several non-cichlids in Lake Victoria have only reached stage 2. It might be imagined that no evolutionary incentive would now exist to progress beyond this stage, and perhaps when lakes are small (and sheltered) this is indeed the case. But in large lakes there will presumably come a time when random feeding movements have carried fishes so far from river mouths that they will be unable to realise their reproductive potential. One must assume that in the large lakes, especially when mouths of affluent rivers are widely-spaced on the shore, such a condition must exist, and that accordingly there will be in the lake considerable numbers of wandering, sexually advanced fishes which are unable to breed unless they can perceive and enter a river. Whether they recognize a river by the composition or by the movement of its water, we may expect the number of fishes ascending it to be related to the amount of water it discharges into the lake. Such a condition apparently exists in Lake Victoria today ; throughout the year sexually advanced fishes of several species are caught in widely varied habitats in the lake (E.A.F.R.O.) ; and, although individuals of certain of these species enter rivers throughout the year, they do so in greatest numbers during the equinoctial rains, and most abundantly in the longer rains (see Garrod, 1957 a, and Whitehead, 1959).

It may be expected therefore that in large lakes it will be of adaptive value for species in this evolutionary stage to modify their habits so as to be able to utilize breeding sites in the lake itself. The first sites to be chosen will presumably be those which most closely resemble the accustomed ones in rivers, namely shores where there is vigorous water movement (see Welch, 1950, p. 144). Ecological studies in Lake Victoria have already demonstrated

that several of the same species of insects inhabiting turbulent regions of rivers, occur also in the lake on rocky shores (e.g. species of *Neoperla*, *Afronurus*, *Euthraulus*, *Metacnemis*, *Platycypha*, *Phanostoma* and *Cheumatopsyche*), whereas others are common to both slowly-flowing rivers and exposed sandy shores (e.g. *Crenigomphus*, *Paragomphus* and *Phyllomacromia*). It is therefore in such sites that we may expect species in stage 3 to breed.

Once the habit of breeding in the lake, albeit in river-like sites, has been established, the most important step will have been taken towards becoming a lacustrine species. Subsequently, and so long as the lacustrine breeding sites are encountered more often than mouths of suitable rivers, it may be expected that species will become progressively better adapted to lake breeding, and less dependent on rivers. Finally, when the positive taxis to river water is lost by breeding individuals, a species may be said to have become truly lacustrine.

An indication of which species in Lake Victoria have progressed to stage 3 or beyond, should be obtained from *upstream* catches in fish weirs. Those species known to be common in lake and river, but which do not ascend rivers in large numbers to breed, must be assumed to breed in the lake. Examination of the appropriate records (see Whitehead, 1959) reveals that two such species are *Mormyrus kannume* and *Bagrus docmac*, which together comprise the most important non-cichlid food fishes of Lake Victoria.

As we have seen, data on the food of these two species has supported the view that they at present exist in stage 3. Juveniles of both species are known to live in turbulent regions of the Victoria Nile, where they feed on lithophilic insects. The food of larger individuals in the river is different : *M. kannume* feeds more in sheltered sites on chironomid larvae, and *B. docmac* on fishes. Juveniles of these species have hardly ever been found in the lake (no serious collections have been made on rocky shores) but amongst larger fishes the feeding-habits change in a well-marked fashion according to their size. In the lake, *M. kannume* and *B. docmac* feed progressively less on insects associated with a hard bottom as they grow older. There is thus strong presumptive evidence from independent sources to suggest that in the lake these species breed on rocky shores —one of the few habitats which cannot be sampled by ordinary means.

If confirmation of this is obtained, it will show *M. kannume* and *B. docmac* to be relatively highly evolved in this respect amongst non-cichlid fishes of the lake. Furthermore it will augur well for their future exploitation, since not only will they escape the tremendous annual toll exacted by fishermen on those fishes which ascend rivers to breed, but they will breed in one of the few sites almost immune from predation or human interference.

Having described the temporal context in which it is appropriate to consider the non-cichlid fishes, we may now discuss their main food preferences. From what has already been said in previous sections, it can be seen that probably no two non-cichlid fishes occupy exactly the same feeding niche, unless perhaps at some particular place and time, as for instance when several surface-feeders may be gorging on emerging *Povilla*, or perhaps when juveniles are feeding on lithophilic insects in a river. But it must be remembered that

many *Haplochromis* utilize the same foods as non-cichlids and that, until precise comparisons can be made, the amount of interspecific competition for food cannot be accurately assessed. This question will be mentioned later.

The only non-cichlids which feed heavily on epilithic and epiphytic algae are *Labeo victorianus* and *Garra johnstoni*, both of which have mouths highly specialized for the purpose. Of the two, *Garra* apparently includes more lithophilic insects in its diet.

The principal plant-eating species are *Alestes jacksoni* and *A. sadleri*, both of which supplement this food with significant quantities of insects, most of which are taken from the surface. These two species differ in the sizes of the insects they eat. *Barbus altianalis*, although primarily a mollusc-eater, also utilizes higher aquatic plants to some extent, particularly it seems in rivers.

Engraulicypris argenteus is the only specialized pelagic feeder on zooplankton, although small surface-feeders like *Aplocheilichthys pumilus* may ingest considerable amounts with other food. The latter species, however, is probably restricted to marginal vegetation. It is a remarkable fact that

TABLE 59

Proportion of fishes containing food in lake or river.

Species	Percentage with food in stomach	Numbers examined
Gnathonemus victoriae	99·8	405
Alestes sadleri†	95·7	117
*Mastacembelus victoriae**	95·4	194
Mormyrus kannume	93·6	2793
Gnathonemus longibarbis	93·5	107
Protopterus aethiopicus	93·4	257
Alestes jacksoni	88·3	617
*Clariallabes petricola**	86·7	285
Engraulicypris argenteus	85·7	126
Synodontis victoriae	85·5	235
Bagrus docmac	80·6	1389
Barbus altianalis radcliffi	78·0	405
Clarias mossambicus	55·4	392
Schilbe mystus	49·3	426

NOTE.—All samples from Lake Victoria except two from Victoria Nile*, and one from Lake Kyoga†.

several records exist of *Clarias mossambicus* having gorged on zooplankton, but they are so infrequent as to make it unlikely that the gill-rakers are a functional specialization for this purpose (see Greenwood, 1957 b).

If the bulk of species is considered, it is clear that insects form by far the most important food of non-cichlids in the Lake Victoria basin. There are hardly any species which do not at some time include insects in their diet, whereas there are many (especially Mormyridae and young fishes) for which they provide virtually the entire food. In one respect, it is misleading to classify all insectivorous fishes together, since some (e.g. *Alestes*, *Barbus*, *Schilbe*, *Synodontis*, *Aplocheilichthys*) derive substantial proportions from the surface, whereas others (e.g. Mormyridae, *Clariallabes*, *Mastacembelus*) feed almost exclusively on the bottom. However, the broad explanation for the

importance of insects as food for carnivorous fishes seems to be, not that they are favoured *per se*, but that at the surface, in marginal vegetation, and on the bottom, they constitute the only numerous and available prey of an appropriate size—except molluscs which, on account of their shells require specialized treatment to be exploited. These considerations apply in particular to habitats occupied by young fishes, since the latter are mostly insectivorous. Insects are apparently the most widespread prey, and require of their predators the least specialization of feeding habits. It is consistent with these conclusions that several mormyrids include demersal fish eggs in their diets.

Whatever may have been the background for development of the insectivorous habit, its adoption is evidently leading to specializations in certain species. Chironomid larvae are a preferred food of most Mormyridae (as of many fishes in the White Nile (see Lewis, 1957)), particularly *Mormyrus kannume* which, in utilizing this prey, has become somewhat specialized as a soft bottom feeder. But, although these mormyrids can be said to show incipient specialization in this respect, it is important to emphasize that they nevertheless exhibit great flexibility of trophic behaviour when deprived of their preferred food. In this they differ markedly from *Mastacembelus victoriae* which is probably one of the very few stenophagous insectivores in the lake.

Two factors which have probably permitted this loss of adaptability in *M. victoriae* are first, that it is of a shape and size such that it can remain in the same habitat throughout its life, and second, that its habitat is much the same in lakes and rivers. In both these respects, however, *M. victoriae* must be regarded as a special case ; in general, the ecological conditions prevailing in the area do not encourage specialization of feeding habits. In the first place, most fishes " grow out " of their juvenile food and come to require progressively larger prey, and in the second, many range over a wide variety of aquatic habitats in all of which they may feed. The absence of effective ecological barriers between varied river and lake environments will result in continual interchange between populations of the same species utilizing different foods.

The wide occurrence of facultative feeding habits has important implications when the use of fishes for biological control is envisaged. As we have seen, in appropriate habitats, at least eight species of fish feed on larvae or pupae of *Simulium*. In addition to the four mormyrids mentioned on page 44, these are *Barbus portali*, *Clariallabes petricola*, *Synodontis victoriae* and *S. afro-fischeri*. Probably other lithophilic insectivores, such as *Amphilius*, young *Bagrus*, etc., also feed on them from time to time. (*Mastacembelus* is unlikely to do so because it evidently feeds amongst the interstices of stones rather than on their upper surfaces.) But, whereas it is one matter to record these species as predators of *Simulium*, it is quite another to recommend their use for biological control. As most, if not all of them have widely adaptable feeding habits, it is probable that they would quickly change to some other food as soon as *Simulium* larvae became even slightly difficult to obtain. It is therefore unlikely that they could effectively maintain *Simulium* populations at a low level.

Non-cichlids for which molluscs provide the principal food are, in order of the preference they show, adult *Protopterus aethiopicus*, *Synodontis victoriae*, and *Barbus altianlis*. *Protopterus* is evidently the most efficient of these, since it can crush molluscs of any size, including the largest individuals of *Mutela bourguignati*. *Barbus* also crushes shells, but is probably unable to deal with such large species. *Synodontis victoriae* exhibits a specialization in that it is able to remove the flesh and opercula from the shells of gastropods. Another fish which has apparently developed this ability is *Marcusenius grahami*, in which however Gastropoda only provide main contents in 6 per cent. Certain other fishes, including *Synodontis afro-fischeri* and *Clarias mossambicus*, eat gastropods in very small quantities, but ingest the entire shells.

In all mollusc-eating fishes, *Melanoides tuberculata* and *Bellamya* predominate as food, which probably indicates that they are the most abundant gastropods in the lake. Pelecypods are eaten far less than gastropods—small species mainly by *S. victoriae*, both small and large by *P. aethiopicus*. The latter seems to be the only effective predator in the lake of *Etheria*, *Caelatura* and *Mutela*. None of the mollusc-eating species shows particularly lacustrine specializations, but as habitats suitable for certain molluscs are probably more extensive in the lake, it may be that species possessing this potentiality feed more heavily on them in the lake than in the river. In this connection it is of interest to note that *B. altianalis*, a stage 2 fish breeding in rivers but feeding in the lake (on molluscs), has presumably been the agent responsible for the introduction of *Mutela bourguignati* into the lake (see Fryer, 1959 a).

There are few piscivorous species of non-cichlids. If we exclude scavengers or damagers of fish, such as *Protopterus aethiopicus* and *Alestes jacksoni*, and also insectivorous species which sometimes feed on fish eggs or fry, we find that fishes (almost entirely *Haplochromis*) provide an important food for only three species, namely, *Bagrus docmac*, *Clarias mossambicus* and *Schilbe mystus*, and to a much lesser extent for a fourth, *Mormyrus macrocephalus*. Of these, *B. docmac* is probably the most specialized lacustrine fish, and must be regarded as the main predator of *Haplochromis* in the lake. *C. mossambicus* feeds relatively more on larger insects and arthropods, whereas *S. mystus* feeds more at the surface—utilizing more *Engraulicypris* and surface insects.

There are, then, very few predatory fishes utilizing the *Haplochromis*. Predatory *Haplochromis* and fish-eating birds do, of course, occupy this niche, but from an economic viewpoint neither group renders the *Haplochromis* resources widely available to man in a satisfactory form. At present only *Bagrus docmac* can be said to be achieving this. It is this state of apparent unbalance which would seem to provide an argument for the introduction of a larger predatory fish, such as *Lates*, into Lake Victoria. It has already been remarked that *Lates* would perhaps assist in making *Alestes* more available to man than it is at present. It is hardly necessary to stress, however, that no such introductions should be made until it can be reasonably predicted that, with regard to its feeding habits and breeding behaviour, *Lates* would benefit, and not detract from, the existing productivity of the lake. One important fact to be borne in mind is that at present there seem to be no

predatory fishes which feed other than occasionally on adult *Tilapia*, whereas *Lates* is known to do so to a small extent when a certain size (Stoneman, 1959). Any change which significally increases predation on *Tilapia* is clearly to be avoided. In this connection, it would be valuable to determine the extent of present predation on young *Tilapia* in the lake—a subject not covered by the present data, since predatory fishes were seldom caught near *Tilapia* nurseries. The proposed introduction of *Lates* into Lake Victoria has recently been discussed in detail by Fryer (1960) who, in a closely-argued review, concludes that, both ecologically and economically, such a step would be very undesirable.

Where the introduction of alien fishes is concerned, it is also necessary to know more about the non-human predators of non-cichlids. The available evidence indicates that, apart perhaps from crocodiles and otters, non-cichlids have few predators, most piscivorous birds and fishes concentrating instead on *Haplochromis*. But data are now needed on the predators of juvenile non-cichlids near their breeding sites, and also on the food of little-studied piscivores such as otters. The faeces of the latter are readily found, and probably provide the best means of obtaining the required information.

In conclusion, we may briefly consider the ways in which the present data throw light on the subject of inter-specific competition for food—a subject which has been discussed at length by several authors (e.g. Hartley, 1948 ; Larkin, 1956 ; Fryer, 1957, 1959 b). It must first be emphasized, however, that their present feeding-habits in Lake Victoria are unlikely to indicate how ecological divergence of the non-cichlids took place. The conclusion has already been reached that the present species evolved elsewhere, and have since become secondarily associated in a new habitat. Ecologically, the result is much the same whether they evolved in different lakes or rivers, or in micro-isolation within a single lake (see Worthington, 1954). The question is whether, having become associated, they now compete to a significant extent for food.

A full understanding of this problem must, as Worthington has remarked (1954), await critical studies of the behaviour of the species concerned. But we may nevertheless note several factors which would operate to reduce the effects of such competition. Firstly, although most species are unspecialized feeders, it has nevertheless been found that no two regularly have exactly the same diet ; and even in rare cases when two species do eat the same food, they usually collect it in different ways, as is well illustrated by the mollusc-eaters. Furthermore, it is possible that greater taxonomic knowledge of the prey organisms may reveal wider differences between predators than are now suspected. Secondly, juveniles and adults of one species often live in different habitats and eat different food ; and thirdly, many species are facultative feeders able to range freely over a feeding ground of tremendous extent and variety.

Accordingly, there is one species in which intraspecific competition for food might be expected to occur between juveniles and adults, namely *Mastacembelus victoriae* in the Victoria Nile. Even there, however, several other species feed heavily on lithophilic insects in the same habitat ; so that apparently competition is obviated by an abundance of food.

The available evidence, then, suggests that interspecific competition for food amongst non-cichlids in Lake Victoria plays a very minor part in their ecology. The few species with specialized feeding habits appear to enjoy a superabundance of food, whereas the others achieve the same object by remaining mobile and facultative.

SUMMARY

A study has been made of the food of non-cichlid fishes in Lake Victoria and its associated rivers. The method of food assessment adopted recognized both the occurrence and volume of food items and proved suitable for the statistical analyses required. The data, which involved composite records for over nine thousand fishes were analysed with Hollerith machines. Respects in which the problem is particularly well suited for such analysis are mentioned.

The food of twenty-six species is described. Most fishes for which data are adequate to demonstrate this are facultative feeders and their diet is liable to vary significantly according to their size, their feeding-grounds or to the age of the moon. Attention is drawn to a factor which might cause lunar periodicity in catches of freshwater pelagic fishes.

In general the organisms eaten by carnivorous fishes seem to be determined by the size of the prey and its position in the aquatic environment and this is regarded as a reason why so many species in the lake are insectivorous. Eight species of fishes have been found to feed on immature stages of *Simulium* in rivers. Ontogenetic changes in feeding behaviour have been analyzed in detail for an insectivore *Mormyrus kannume* and a piscivore *Bagrus docmac*, and are advanced as evidence for the view that these species are relatively well adapted to the lacustrine environment and that they may breed on rocky shores there. Only three non-cichlids are extensively piscivorous. These feed very largely on *Haplochromis*, slightly on *Engraulicypris* and hardly at all on *Tilapia*. The possible introduction of *Lates* into the lake is discussed in the light of these findings.

The evolutionary stages involved in the colonization of lakes from rivers are discussed with particular reference to breeding habits and food. It is concluded that non-cichlids in Lake Victoria have not progressed far towards becoming adapted to the lake environment.

Several fishes and birds feed on *Engraulicypris argenteus* but otherwise natural predators of non-cichlids are few ; amongst these crocodiles are probably the most important. The question of interspecific competition for food is discussed.

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ADDENDUM

Since the foregoing paper was completed, an opportunity was provided to test its main thesis—namely that rocky shores in Lake Victoria provide breeding sites for non-cichlids in stage 3 of the evolutionary scale mentioned on p. 87. A short strip of rocky, wave-washed shoreline on the Entebbe peninsula was treated with poison, and the fishes were collected from it. The results amply confirm expectation and have been reported briefly elsewhere (Corbet, 1960 c). They do not necessitate any alterations being made to the foregoing paper, but, on the contrary, support the view that ontogenetic changes in feeding behaviour can provide useful indications of the preferred habitat of juvenile fishes. The purpose of this Addendum is to record briefly the food of the eight species of non-cichlids collected on the rocky shore, and to comment on the significance of these results in the light of what has been said previously.

MORMYRUS KANNUME

Eight fishes (11–20 cm.) were collected. All contained food, and all save one sand grains. The main food was chironomid larvae (occurrence 7 ; main contents 4), *Povilla* larvae (5 ; 2) and free-living Ephemeroptera larvae (1 ; 1) including *Caenis* and *Euthraulus*, probably *bugandensis*. Other foods were Trichoptera larvae (5), including *Ecnomus* (3), *Phanostoma* (1), *Cheumatopsyche falcifera* (1) and Hydroptilidae (1), an aquatic bug, *Sphaerodema* (1), Hydracarina (2) and Ostracoda (2).

These fishes had been feeding on lithophilic insects, amongst which chironomid larvae provided the main item. It is interesting to note that the adult specialization is foreshadowed at this early stage.

ENGRAULICYPRIS ARGENTEUS

One fish (59 mm.) had fed mainly on Conchostraca, but also on chironomid larvae.

BAGRUS DOCMAC

Forty-one fishes (3–16 cm.) were collected, of which thirty-nine contained food. It may be noted that these fishes cover the size-range for which no data existed previously from the lake. As they exhibit changes in food with size even within the size-range considered, results have been presented both separately and in combination in Table 60.

TABLE 60

Bagrus docmac : occurrence and (main contents) on a rocky shore in Lake Victoria.

Food	Size-group in cm. 3–7	8–16	Total 3–16
Insects	20 (10)	16 (4)	36 (14)
Chironomid larvae	11	3	14
Povilla larvae	—	6 (1)	6 (1)
Ephemeroptera : free-living larvae	12 (4)	4	16 (4)
Trichoptera larvae	11	7	18
Ecnomus	11	5	16
Trichoptera pupae	—	1	1
Coleoptera larvae	1	—	1
Ostracoda	5	—	5
Copepoda	4	—	4
Caridina	14 (10)	13 (8)	27 (18)
Potamon	1	3 (2)	4 (2)
Fishes	—	5 (3)	5 (3)
Cichlidae	—	2 (1)	2 (1)
Non-cichlids	—	3 (2)	3 (2)
Terrestrial insects	—	3 (1)	3 (1)
Number of fishes containing food	21	18	39

Fishes of both size-groups had fed mainly on lithophilic insects and *Caridina*. Those below 8 cm. had fed more on larvae of Ephemeroptera, chironomids and Trichoptera and on Ostracoda and Copepoda, and had eaten no fishes. Those of 8 cm. and above had fed more heavily on larger insects (*Povilla* larvae and terrestrial Hemiptera—Homoptera), and on *Potamon*. The latter were young *P. niloticus* of carapace-width 7–10 mm. Fishes eaten by *Bagrus* were all digested and included a cichlid of 15 mm. (in a fish of 8 cm.), a siluroid of 16 mm. (16 cm.), a *Clarias* of 40 mm. (10 cm.) and a *Bagrus* of 44 mm. (13 cm.).

Lithophilic insects eaten by both size-groups included *Neoperla spio*, *Euthraulus* (probably *bugandensis*), *Afronurus ugandanus*, *Baetis*, and *Cheumatopsyche falcifera*. A *Povilla* larva had been ingested with its case.

These results agree closely with those obtained from the Victoria Nile (Table 38) and show that the ontogenetic changes recorded amongst larger fishes in the lake (Figs. 14–19) represent a continuation of trends already established in juveniles.

CLARIAS MOSSAMBICUS

Fifteen fishes (3–14 cm.) were collected. Of the fourteen examined (3–14 cm.) all contained food.

The food was extremely varied but consisted in the main of aquatic insects (occurrence 14 ; main contents 11), free-living Ephemeroptera larvae (9 ; 3), fishes (3 ; 2), *Potamon* (2 ; 2) and aquatic Coleoptera (5 ; 1).

Aquatic insects included chironomid larvae (6) ; *Neoperla spio, Euthraulus, Caenis, Ecnomus,* Hydroptilidae and a notonectid larva. Occasional items were Ostracoda (6), Copepoda (1), Conchostraca (1), *Caridina* (early larvae) (1), Hydracarina (1), entire shells of *Biomphalaria* (2) and a fish egg (1).

No clear cut change of food with size could be discerned. The smallest fish examined (31 mm.) contained a siluroid (probably *Clarias*) of 11 mm. which itself contained only Ostracoda. These results are consistent with those obtained for small *C. mossambicus* elsewhere (see p. 71 *et seq.*) which showed that individuals begin to feed on fishes when about 3 cm. long.

CLARIAS ALLUAUDI (group)

Three fishes (7–10 cm.) were collected. Both of the two examined contained food. One (9 cm.) had eaten free-living Ephemeroptera larvae and a small pelecypod ; and the other (10 cm.) contained only *Caridina*.

CLARIALLABES PETRICOLA

Thirty-four fishes (3–11 cm.) were collected. Of the thirteen examined (3–10 cm.), twelve contained food. The main food consisted of lithophilic insects (occurrence 10 ; main contents 7) and *Caridina* (2 ; 2). The insects comprised free-living Ephemeroptera larvae (3 ; 2), Trichoptera larvae (4 ; 1) ; and Coleoptera larvae (2 ; 1), and included *Neoperla spio, Euthraulus, Ecnomus* and *Cheumatopsyche falcifera*. Occasional items were Ostracoda (3), *Biomphalaria* (2) and Hirudinea (1).

These data show that the food of *C. petricola* in this rocky shore habitat is substantially the same as in the Victoria Nile. In the series from the lake no change of food with size could be discerned.

SYNODONTIS AFRO-FISCHERI

One fish (11 cm.) contained mainly insects, comprising chironomid and hydroptilid larvae, Ostracoda and much unidentifiable slush.

MASTACEMBELUS VICTORIAE

Thirty-one fishes (3–15 cm.) were collected. Thirty were examined and twenty-three contained food. These had been feeding mainly on lithophilic insects (occurrence 18 ; main contents 11)—principally free-living Ephemeroptera larvae (14 ; 10)—*Caridina* (9 ; 6) and fish eggs (2 ; 2). The insects eaten included larvae of *Neoperla spio, Caenis, Baetis, Povilla, Ecnomus* and hydroptilids. A change in diet appeared to occur at about 10 cm., such that fishes above this size fed mainly on *Caridina*, and those below mainly on Ephemeroptera larvae. Apart from this, the feeding habits are closely similar to those exhibited by fishes in the Victoria Nile (see p. 85).

CONCLUSIONS

The results of this collection from a rocky shore strongly emphasize the ecological similarity which exists between this habitat in the lake and turbulent

reaches in associated rivers. Particularly noteworthy are the large numbers of *Clariallabes petricola* and *Mastacembelus victoriae*. The former had not previously been collected from the lake proper, and the latter only in small numbers. The finding that young *Clarias mossambicus* and *C. alluaudi* feed in such a habitat suggests that vigorous water movement may be an attribute of the preferred habitat of juveniles of these species.

This work has not demonstrated that *Mormyrus kannume* breeds on rocky shores, although the evidence presented elsewhere (pp. 27, 41, 88) supports this view as strongly for *M. kannume* as for *Bagrus docmac*, for which confirmation has since been obtained. For the present, however, this must remain an open question.

There can be no reasonable doubt, however, that rocky shores have played, and are playing, an essential role in the colonization of lakes by riverine fishes. It is certain that a systematic study of this habitat would lead to a better understanding of the evolutionary stages involved in this transition.

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THE OXYURID PARASITES (NEMATODA) OF PRIMATES

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(With 14 figures in the text)

Enterobius nycticebi Baylis, 1928 and *E. callithricis* Solomon, 1933 are briefly redescribed and the oxyurid parasites of primates are discussed, additional morphological evidence being presented on many of them when necessary. The parasites are regrouped into two genera, with two subgenera each, thus : *Enterobius* Leach, 1853 with *Enterobius* and *Protenterobius* subgen. nov. (type species *E. nycticebi*) ; *Trypanoxyuris* Vevers, 1923 with *Trypanoxyuris* and *Paraoxyuronema* Artigas, 1937. A trend from a three-lipped mouth opening to a two-lipped is demonstrated within the genus *Trypanoxyuris* and a trend from a "doubled" to "single" spicule is demonstrated within *Enterobius*. It is pointed out that although the trend in *Enterobius* parallels the phylogeny of the hosts in part it does not necessarily establish a phylogeny particularly as there are relatively few records of the parasites. This is clearly demonstrated by recording from which of the genera of living primates oxyurid parasites have been reported. It is argued that "Cameron's Hypothesis"—one species of parasite (*Enterobius* or *Trypanoxyuris*) : one genus of host—appears to hold good in the wild and that there is a tendency in the genus *Enterobius* for the parasites most like the parasites of man to occur in the hosts phylogenetically nearest man. The subfamily Oxyurinae is reviewed and two tribes, Oxyurini and Heteroxynematini, are recognized. It is reported that *Callistoura brygooi* Chabaud and Petter, 1958 does not have a spicule and that the structure described by Chabaud and Petter as such is a modified gubernaculum similar to that found in *Ozolaimus* and related genera. The great similarity between the male tail of *C. brygooi* and *Ozolaimus* is noted and it is suggested that *Callistoura* should be treated as a genus *incertae sedis* until a full study of the subfamily Pharyngodoninae, to which it is clearly related, can be undertaken. Several new synonyms are demonstrated, thus : *Buckleyenterobius dentata* Sandosham, 1950 = *Enterobius lemuris* Baer, 1935 ; *Oxyuris parallela* Linstow, 1908 = *O. polyoon* Linstow, 1909 and is referred to *Enterobius* ; *Oxyuris armata* Kreis, 1940 = *Primasubulura distans* (Rudolphi, 1819).

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INTRODUCTION

The oxyurid parasites of primates, most of which have been referred at one time or another to the genus *Enterobius*, have been considered recently by Sandosham (1950) and Inglis & Díaz-Ungría (1960). Sandosham treated the Old World species in detail and the New World forms in outline only while Inglis & Díaz-Ungría concentrated on the New World species. The results of the two studies do not agree on some points and neither has considered certain species which clearly affect the classification of the group as a whole: particularly *Enterobius nycticebi* Baylis, 1928, *E. callithricis* Solomon, 1933 and *Paraoxyuronema brachytelesi* Artigas, 1937. I have been able to study specimens of all three species and as a result can now propose a classification of the genus *Enterobius* s.l. which appears to be more natural than any put forward heretofore. Before this is done it is necessary to give partial redescriptions of some species.

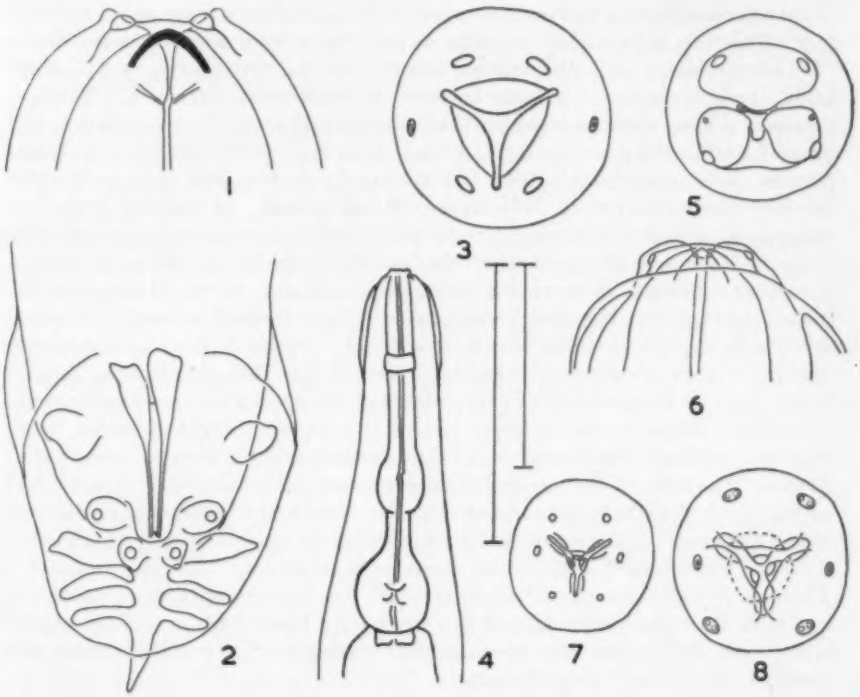
ENTEROBIUS NYCTICEBI Baylis, 1928

The syntypes of this species are in the collections of the British Museum (Natural History), Reg. Nos. 1928.6.18.1–25, one male here selected as Lectotype. They are in a rather poor condition but the head bears at least two pairs of papillae: it is impossible to be sure whether there are more papillae or whether the two pairs are single or double. The mouth opening is surrounded by three lips which are not prominent (Figs 1 & 3), the pharyngeal portions are embedded within the head and the oesophagus possesses a distinct middle bulb (Fig. 4) produced by the presence of a very long isthmus. The posterior end of the male is very characteristic with six pairs of papillae. There is one large, stout pair relatively far anterior to the cloacal opening, one stout, roundish pair just anterior, and lateral to the cloacal opening and a similar, but smaller pair just posterior to the cloacal opening. The body narrows rapidly about the level of the cloacal opening and continues as a distinct, narrow tail which bears three pairs of long, narrow papillae. The whole posterior end carries broad alae, supported by the anterior pair of papillae and the posterior three pairs, beyond which the tip of the tail projects. There is a large flap over the cloacal opening, developed from the anterior lip of the opening. The spicule narrows evenly to a fine point posteriorly and expands anteriorly into a thin flat laterally expanded basal portion (Fig. 2), which is made up from two lobes.

ENTEROBIUS CALLITHRICIS Solomon, 1933

The syntypes are in the collections of the British Museum (Natural History), Reg. Nos. 1933.12.1.9–12, one male here selected as Lectotype. The head

bears two pairs of single papillae and the mouth is bounded by three lips. The dorsal lip is large and the two ventro-lateral lips stand on a platform so that they are slightly fused together at their bases (Figs. 5 & 6). The oesophagus has a long isthmus so that there is a distinct middle bulb as in *E. nycticebi* (Fig. 4) and the pharyngeal portions appear to be free for a small part of their anterior ends. The spicule bears a cap on the anterior end which is expanded laterally on both sides and there is a distinct terminal spike to the male tail which projects beyond the caudal alae.



Figs. 1–4.—*Enterobius nycticebi*. 1. Dorsal view of head; 2. Ventral view of male tail; 3. *En face* view of head. This figure was taken from a head under pressure, lack of specimens prevented me preparing another; 4. Oesophagus.
Figs. 5 & 6.—*Trypanoxyuris callithricis*. 5. *En face* view of head (female); 6. Dorsal view of head.
Fig. 7.—*Trypanoxyuris sciuri, en face* view of head.
Fig. 8.—*Trypanoxyuris sceleratus, en face* view of head. The longer scale line equals 0·5 mm and refers to Fig. 4. All other figures to one scale, shown by the shorter line which represents 0·05 mm.

SYSTEMATIC ANALYSIS OF THE SPECIES

The species to be considered fall into three groups (1) *Enterobius vermicularis, E. anthropopitheci, E. brevicauda, E. foecundus, E. lemuris, E. lerouxi, E. nycticebi, E. pitheci, E. simiae, E. zakiri* and *Buckleyenterobius dentata;* (2)

Trypanoxyuris trypanuris, *T. atelis*, *T. duplicidens*, *T. lagothricis*, *T. minuta*, *Enterobius callithricis*, *E. sceleratus* and *Paraoxyuronema brachytelesi* ; (3) Seven miscellaneous species. The first and second groups are restricted geographically, the first to the Old World and the second to South America. Similarly the two groups are morphologically distinct. The most obvious and previously stressed difference between them is the constant presence of a distinct tail spike projecting beyond the caudal alae of the males of the second group but not of the first, with the exception of *E. nycticebi*. There are other correlated characters: in the second group the spicule shows very little variation from one species to another. It always consists of a well cuticularized blade which bears a cap on its anterior end. This cap is expanded laterally so that the spicule appears rather like a 'T' when viewed from the ventral aspect. In the first group, on the other hand, the spicule shows a large amount of interspecific diversity. There is generally a long, anterior basal portion which is rather poorly cuticularised and plate-like while the posterior rod-like blade is strongly cuticularized. The basal portion varies considerably from one species to another and appears to offer the best characters for the delimitation of the species. In the first group the pharyngeal portions are always buried wholly within the surrounding structure of the head while in the second they always project freely into the buccal cavity. A further difference between the two groups is shown by the structure of the mouth opening and the surrounding lips. This difference is more subtle and difficult to explain than the others considered. In the first group the mouth opening is always surrounded by three distinct lips (Fig. 13, *E. vermicularis*) which are well separated from each other and the spaces between them extend posteriorly almost to the anterior end of the cephalic vesicle—except in *E. nycticebi*—while in the second group the mouth opening is always " terminal ". That is, the shape of the mouth opening can only be determined when studied *en face* since the spaces between the lips are restricted to the extreme anterior end of the head. Thus in the first group the mouth opening can be described as " three-dimensional " while in the second it is effectively " two-dimensional ". The only species in the second group to which this does not apply is *E. callithricis* but even here the ventro-lateral lips are partly fused and, as will be argued later, since this species may be considered " primitive " I would attribute this mouth form to that " primitiveness ".

There are seven further species to be considered: (1) *Oxyuris armata* Kreis, 1940, was described from *Papio hamadryas* in East Africa. No males were available, but, from the description, it is clear that this " species " is indistinguishable from *Primasubulura distans* (Rudolphi, 1819) (see Desportes & Lepesme, 1941 and Inglis, 1958). (2) *Oxyuris parallela* Linstow, 1908 and *O. polyoon* Linstow, 1909 were both described from *Xerus inauris* (in the sense of Ellerman, Morrison-Scott & Hayman, 1953), the first from Segkoma, Kalahari and the second from South West Africa. I have seen the syntypes of both species which are in the Zoologisches Museum der Humboldt-Universität zu Berlin, Cat. Nos. 4722 and 4923 respectively (one female here selected as Lectotype) and they are indistinguishable. Therefore the second name falls as a synonym of the first. The description given of this species, under the name *Enterobius polyoon*, by Leroux (1930) is good and I only give here a figure of the

male tail from the ventral aspect (Fig. 10). The head is typical of the species found in Old World primates. (3) *Enterobius sciuri* Cameron, 1932 from *Sciurus carolinensis* in Scotland and *E. sciuri* Kreis, 1944 from *S. vulgaris* in Switzerland are clearly indistinguishable as well as being homonyms. Sandosham's suggestion that this species was brought to Europe with the importation of the American squirrel has been supported by the report of it by Rausch & Tiner (1948) from America and by the form of the spicule, the presence of a terminal spike to the male tail and by the form of the head, all of which link it with the South American group of species considered above.

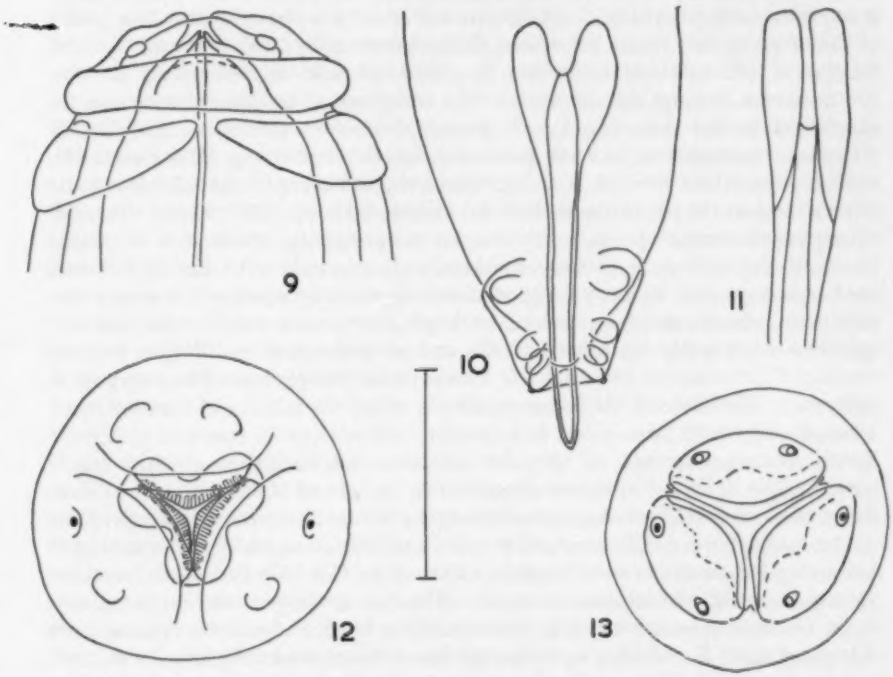


Fig. 9.—*Trypanoxyuris sceleratus*, dorsal view of head.
Fig. 10.—*Enterobius parallela*, ventral view of male tail showing structure of spicule.
Figs. 11 & 12.—*Enterobius lemuris*. 11. Detail of anterior end of spicule ; 12. *En face* view of head.
Fig. 13.—*Enterobius vermicularis*, *en face* view of head. All figures to the same scale. Scale line equals 0·05 mm.

The mouth is surrounded by three lip-lobes and the anterior ends of the pharyngeal portions project freely into the buccal cavity (Fig. 7). The mouth opening is in fact almost indistinguishable from that found in *E. sceleratus*. (4) *E. muris* Yamaguti, 1935 was described from female specimens only from *Rattus norvegicus* in Japan but the later discovery of males led Yamaguti (1941) to refer it to *Syphacia*. I mention this species because Sandosham (1950) did not know of Yamaguti's second paper and continued to refer to *E. muris*.

(5) *Callistoura brygooi* Chabaud and Petter, 1958 from *Lemur macaco* in Madagascar is clearly distinct from all the other oxyurids and need not be considered further here (but see page 118).

SYSTEMATIC GROUPING

The species occurring in Old World hosts form a neat morphological group except for *E. nycticebi*. However from the redescription of that species it is clear that it is most unusual and differs from the typical group in more than simply having a terminal spike to the male tail. The tail is unique in its extreme length, with three pairs of long papillae arising from it. This may be interpreted as a primitive character since it is certain that the shortened tails of the more typical forms have been derived from a long-tailed form. On the other hand *E. nycticebi* resembles *E. callithricis* and *P. brachytelesi* in the presence of a distinct middle bulb to the oesophagus but this character can be attributed to the retention by all three species of a primitive oesophageal structure, comparable to that possessed by the free-living rhabditids. *E. nycticebi* resembles the Old World forms in the structure of the spicule and to some extent in the structure of the head and since the spicule is one of the most conservative characters in South American species, in which it is virtually identical throughout, I propose to classify *E. nycticebi* with the Old World species, recognizing its morphological distinctiveness by placing it in a separate subgenus. In the species occurring in South American hosts the male tail and spicule are virtually identical and all, except perhaps *E. callithricis* but including *P. brachytelesi* (see Inglis & Díaz-Ungría 1960a), have free pharyngeal portions. The male of the latter species is unknown but I will forecast that when found it will have a tail and spicule similar to those found in the other South American species. I therefore propose that the genus *Trypanoxyuris* (*sensu* Inglis & Díaz-Ungría) be expanded to include all these species. Within the genus so formed there are two subgroups which can be separated on the form of the oesophagus: (1) *P. brachytelesi* and *E. callithricis* in which the oesophagus has a very long isthmus and therefore a distinct middle bulb and (2) all the other species, in which the isthmus is short. The two species in the first group also appear to belong together on the structure of the head, *P. brachytelesi* being more advanced than *E. callithricis*. The species of the second subgroup have, with two exceptions, been considered recently by Inglis & Díaz-Ungría (1960) who referred them to the genus *Trypanoxyuris* and showed them to be related in possessing all the characters outlined above. The exceptional species are *E. sceleratus* and *E. sciuri* of which the first is characterized by a complicated cephalic vesicle which is divided into a series of lobes (see Cameron, 1929, Figs. 19–21 and Figs. 8 & 9 in the present paper.) However even in this species the pharyngeal portions are free at their anterior ends (Fig. 8), the mouth opening is virtually identical with that of *E. scelaratus*, although with a simple cephalic vesicle. I propose to include both these species in the second subgroup of the genus *Trypanoxyuris*: both subgroups being treated as subgenera.

The two major groups will therefore, be treated as genera, *Enterobius* for the Old World species and *Trypanoxyuris* for the New World species. This grouping has already been foreshadowed, in part, by Buckley (1931), Baer (1935) and

Sandosham (1950). Buckley suggested that *T. lagothricis* and *T. duplicidens*, both of which he had just described as new, might later warrant generic separation from the other species then referred to the genus *Enterobius* while Baer included *T. atelis* in suggesting the possibility of introducing a new genus. Later Sandosham grouped all three species with his new species *Buckleyenterobius dentata* in a distinct genus. However, *B. dentata* was described by Sandosham as having three teeth at the anterior end of the oesophagus and was, for this reason, made the type of the genus *Buckleyenterobius* Sandosham, 1950. I have seen the type and paratypes (London School of Hygiene and Tropical Medicine, Coll. No. 280) and such teeth do not exist. There are three specimens, all females in an extremely bad condition, only one of which still has a head. The head in that specimen is identical with that of *E. lemuris* and it appears probable that Sandosham has misinterpreted the finely striated cuticular structures at the anterior end of the oesophagus, —described by Chabaud & Petter (1958) from *E. lemuris*—as teeth. The presence of these structures and the identity of structure between the heads of the two " species " has been confirmed by studying some of the specimens of Chabaud & Petter (Fig. 12). Sandosham also lays stress in distingishing his species on the relative length of the oesophagus and the form of the vagina. The oesophagus is certainly relatively longer in his specimens than in *E. lemuris* but the specimens are in such an extremely poor condition that it is difficult to accept that this and the form of the vagina are of any value as systematic characters. I therefore not only do not accept *Buckleyenterobius* as a distinct genus but I consider *B. dentata* to be a synonym of *E. lemuris*.

In 1951 Skrjabin *et al* proposed the genus *Odontorobius* for *T. atelis*, *T. duplicidens* and *T. lagothricis*. This also is a synonym of *Trypanoxyuris*. Kreis (1932) described *Oxyuronema atelophora* sp. et gen. nov. from a mixed series of specimens. Inglis & Díaz-Ungría (1960) selected a lectotype indistinguishable from *T. atelis* so that *Oxyuronema* is also a synonym of *Trypanoxyuris*. Artigas (1937) described *Paraoxyuronema brachytelesi* sp. et gen. nov., recorded only by Inglis & Díaz-Ungría (1960 a) since then, so this generic name is the only one available for the second subgenus of *Trypanoxyuris*. The family Oxyuronemidae proposed by Artigas for *Oxyuronema* and *Paraoxyuronema* has not been accepted by any other author and is not accepted here.

The systematic groupings proposed are therefore,

Genus *ENTEROBIUS* Leach, in Baird, 1853

Oxyuridae: Oxyurinae: head with three distinct lips and four single cephalic papillae; pharyngeal portions of oesophagus fully embedded in surrounding tissue of head; cuticle at anterior end of body inflated as cephalic vesicle; lateral alae run full length of body. Male: spicule narrow and well cuticularized posteriorly with thin, flat, poorly cuticularized, plate-like basal portion which is generally much wider than blade; no terminal spike to tail—except in *E. nycticebi;* posterior end with well developed caudal alae supported by long narrow papillae.

Type species: *Enterobius vermicularis* Leach, 1853.

Hosts and Geographical Distribution: Old World Primates with one species in squirrels.

Subgenus *Enterobius*

Head with three large lips; oesophagus with short isthmus. Male: no terminal spike projecting beyond caudal alae; no long tail with long papillae.

The following species are referred to this subgenus:
E. (*E.*) *vermicularis* Leach, 1853; *E.* (*E.*) *bipapillata* (Gedoelst, 1916) Baylis, 1923; *E.* (*E.*) *brevicauda* Sandosham, 1950; *E.* (*E.*) *anthropopitheci* (Gedoelst, 1916) Travassos, 1925; *E.* (*E.*) *buckleyi* Sandosham, 1950; (?) *E.* (*E.*) *faecundus* (Linstow, 1879) Travassos, 1925, sp. inq.; *E.* (*E.*) *lemuris* Baer, 1935 (syn. *Buckley-enterobius dentata* Sandosham, 1950); *E.* (*E.*) *lerouxi* Sandosham, 1950; *E.* (*E.*) *pitheci* Cameron, 1929; *E.* (*E.*) *parallela* (Linstow, 1908) comb. nov. (syn. *E. polyoon* (Linstow, 1909) Leroux, 1930); *E.* (*E.*) *zakiri* Siddigi and Mirza, 1956.

E. simiae (MacCallum, 1921) Travassos, 1925 was rightly treated by Sandosham as a *nomen inquirendum*; it is better to treat it, and probably *E. faecundus* also, as *nomina dubia*.

Subgenus **PROTENTEROBIUS** subgen. nov.

Head with three small lips; oesophagus with long isthmus; Male: terminal spike projecting beyond caudal alae; long tail with three pairs of long narrow papillae.

Type species: *Enterobius* (*Protenterobius*) *nycticebi* (Baylis, 1928) comb. nov.

Host and Geographical Distribution: Lorises in Sarawak and Malaya (I have seen the specimens reported by Cameron, 1929 from Malaya and they certainly belong to this genus, although possibly they are not conspecific with *E. nycticebi* but as only female specimens are present it is impossible to know).

Genus *TRYPANOXYURIS* Vevers, 1923

Oxyuridae: Oxyurinae: mouth complex with three to two lip-lobes; head frequently bears eight papillae arranged in two circles of four; pharyngeal portions project into buccal cavity; cuticle inflated as a cephalic vesicle; lateral alae run full length of body. Male: spicule T-shaped with anterior cap which is expanded laterally; terminal spike to tail; well developed caudal alae supported by long narrow papillae.

Type species: *Trypanoxyuris trypanuris* Vevers, 1923.

Hosts and Geographical Distribution: South American primates and one species in squirrels.

Subgenus *Trypanoxyuris*

Oesophagus with a short isthmus; head frequently bears eight single papillae in two circles.

The following species are referred to this subgenus:
T. (*T.*) *trypanuris* Vevers, 1923; *T.* (*T.*) *atelis* (Cameron, 1929) Inglis & Díaz-Ungría, 1960; *T.* (*T.*) *duplicidens* (Buckley, 1931) I. & D.-U., 1960; *T.* (*T.*)

lagothricis (Buckley, 1931) I. & D.-U., 1960; *T.* (*T.*) *interlabiata* (Sandosham, 1950), I. & D.-U., 1960; *T.* (*T.*) *minuta* (Schneider, 1866), I. & D.-U., 1960; *T.* (*T.*) *sceleratus* (Travassos, 1925) comb. nov., *T.* (*T.*) *sciuri* (Cameron, 1931) comb. nov. (syn. & homonym *E. sciuri* Kreis, 1944).

Subgenus **PARAOXYURONEMA** Artigas, 1937 (new as a subgenus)

Oesophagus with a long isthmus.

Type species: *Trypanoxyuris* (*Paraoxyuronema*) *brachytelesi* (Artigas, 1937) comb. nov.

Other species: *Trypanoxyuris* (*Paraoxyuronema*) *callithricis* (Solomon, 1933) comb. nov.

TRENDS AND PHYLOGENETIC RELATIONSHIPS

In the classification I have treated the existence of a middle bulb to the oesophagus as a primitive character. It may from this be argued that I interpret, or should interpret, the two major groups as having arisen from the same ancestral form or group of forms. This may be so but the evidence is insufficent to establish it as a fact or even as a reasonable hypothesis. In dealing with these groups of species the same difficulties are encountered as in the grouping of the primate hosts themselves. Thus, to quote Patterson (1957): "They (Old and New World Monkeys) have almost certainly been derived independently from prosimian ancestors living in widely separated areas, and these ancestors may have belonged to different prosimian groups . . . . . The advanced characters common to the two (groups) may well have been acquired in parallel." This statement applies equally to the species under consideration here. There is ample morphological evidence to warrant the recognition of two groups with two subgroups each but it is impossible to know whether the major groups are sufficiently close to warrant treating the entire complex as one genus. That the short tails characteristic of these species have been derived from the long tails of some ancestral form or forms cannot be doubted but to argue from that that it was the same ancestral form in both cases is invalid. It is worth noting that in both the subgroups found in South America a two-lipped form of the mouth opening has appeared, in *T. atelis*, *T. duplicidens* and *T. lagothricis* on the one hand and *T. brachytelesi* on the other. Such a dorso-ventral symmetry is rare in nematodes and its independent appearance in two related lines suggests an inherent tendency towards its appearance: such a tendency is never seen in the Old World species. In addition the development of the mouth opening and the pharyngeal portions has been totally different between the Old and New World parasites. In the Old World forms the specialization has been restricted mainly to the form of the spicule and, to a lesser extent the male tail as a whole, while in the New World forms the specialization is almost all restricted to the head with virtually no variation in the form of the spicule and male tail. All this argues for the independent origin of the two groups and, although this cannot be established with certainty, it appears best to recognize two genera with two subgenera each, as has been done above.

It is possible to demonstrate a morphological trend in the subgenus *Trypanoxyuris* from a three-lipped mouth opening to a two-lipped condition, as has been done by Inglis & Díaz-Ungría (1960) but this cannot be taken as demonstrating a phylogeny. The only conclusion that can definitely be drawn about the group is that it represents a group of related species which have probably radiated from some common stock. The same appears to be true of the species referred to the subgenus *Enterobius* in which almost the only characters on which an analysis can be based are those shown by the structure of the spicule. If it is taken that the single spicule has appeared by the fusion of two originally paired spicules, as appears certain, the spicule in which the anterior plate-like portion is most markedly divided into two parts may be considered the most primitive. It must be stressed that there is no reason to believe that the single spicule is the result of the loss of a spicule. The validity of using the structure of the spicule in this way is supported by the structure of the spicule in *E. nycticebi* which can be considered " primitive " on the basis of other characters and in which the spicule is very strongly divided (Figs. 2 & 14, j).

The trends referred to are represented in Fig. 14: that apparent in *Trypanoxyuris* is shown on the left-hand side of the figure and is largely based on the evidence presented by Inglis & Díaz-Ungría (1960) in conjunction with the new evidence set out above. The trend in the structure of the spicule in *Enterobius* is shown on the right-hand side of the same figure. This is based almost wholly on the figures published by Sandosham (1950), also in conjunction with the new evidence set out above. I had hoped to restudy Sandosham's material since he did not appreciate the value of the form of the spicules as a systematic character but, although the specimens are available in the collections of the London School of Hygiene and Tropical Medicine their condition is such that it is impossible to obtain any information of value. Almost all the specimens are badly damaged and deeply stained.

Within the genus *Trypanoxyuris* there is a clear trend towards a two-lipped mouth opening, a trend demonstrated in the figure. (Fig. 14, a–h). In the subgenus *Paraoxyuronema* the structure of the head in *T.* (*P.*) *brachytelesi* (b) has been produced by the fusion of the ventro-lateral lips: a suggestion supported by the form of the mouth opening and the underlying buccal cavity of *brachytelesi* in which the ventral ' lip ' is larger and more strongly subdivided than the dorsal. Along the other line, subgenus *Trypanoxyuris*, the two-lipped form characteristic of *T. atelis* (g) and *T. lagothricis duplicidens* (h) appears to have been produced by the suppression of the left ventro-lateral lip with a corresponding increase and shift of the right lip. This is suggested by the form of the mouth in *T. interlabiata* (f) in which the left ventro-lateral lip becomes more and more reduced during development (see Inglis & Díaz-Ungría, 1960). However, this head form is clearly very specialized and it is possible that the two-lipped head forms have been derived independently from the others in the *Trypanoxyuris* group, perhaps from a form similar to that in *T. brachytelesi*.

Within the genus *Enterobius* the trend towards increased fusion of the spicule is clear but it is difficult to analyse this functionally as has been done by Inglis & Díaz-Ungría (1960) for the head forms in *Trypanoxyuris*. The major

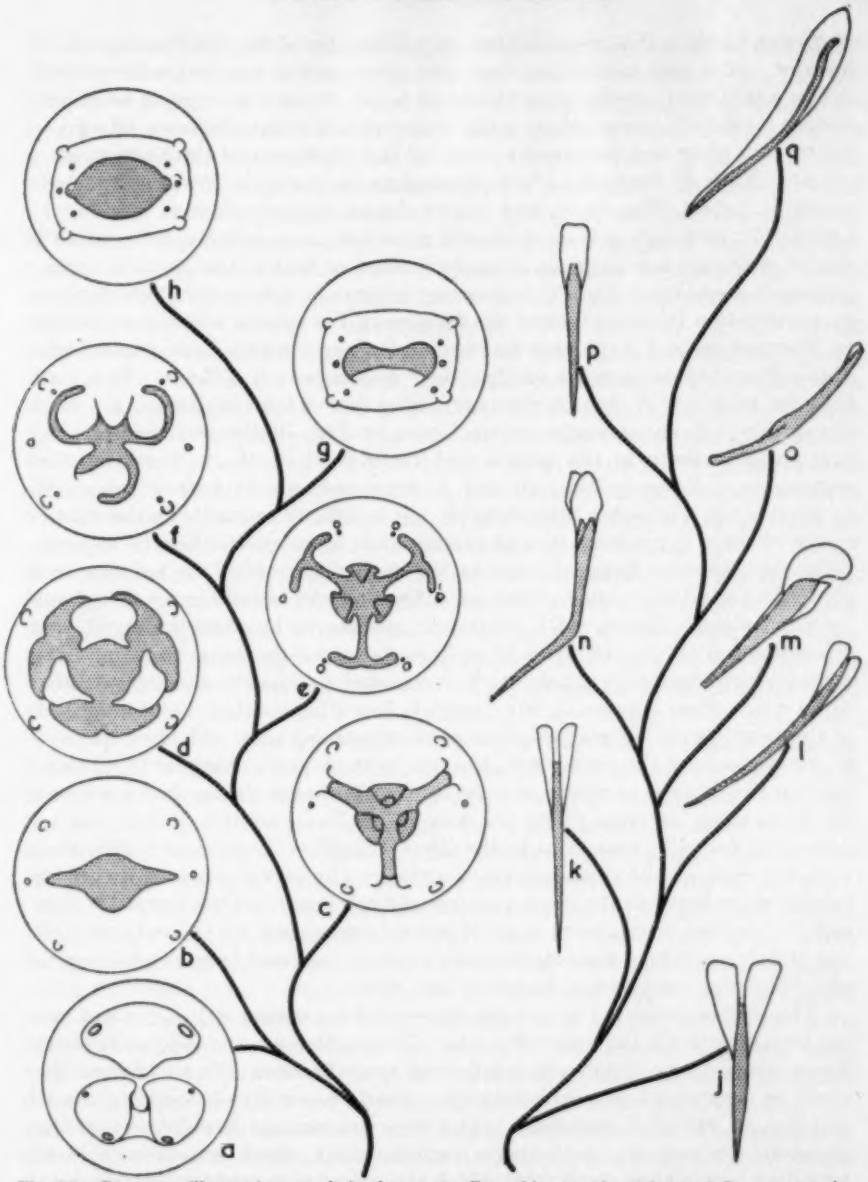


Fig. 14.—Diagrams illustrating trends in the genera *Enterobius* (on the right) and *Trypanoxyuris* (on the left).

a, *T. callithricis*; b, *T. brachytelesi*; c, *T. scleratus*; d, *T. minutus*; e, *T. trypanuris*; f, *T. interlabiata*; g, *T. duplicidens* and *T. lagothricis*; h, *T. atelis*; all from females. b based on Inglis and Díaz-Ungría (1960 a), d–h based on Inglis & Díaz-Ungría (1960); others original. j, *E. nycticebi*; k, *E. lemuris*; l, *E. bipapillatus*; m, *E. brevicauda*; n, *E. buckleyi*; o, *E. anthropopitheci*; p, *E. vermicularis*; q, *E. lerouxi*; l–o and q based on Sandosham (1950); others original. Note that the two trends are illustrated on the same figure for convenience and are not related, that on the left representing the modification of the head in *Trypanoxyuris* while that on the right illustrates the modification of the spicule in *Enterobius*.

stumbling block is that we still have very little idea of the full function of the spicules. It is easy to say that they play some part in copulation but until it can be established exactly what their role is any attempt to suggest functional reasons for spicular morphology must be barren and unsatisfactory. However, the trend is clear and does tend to parallel the phylogeny of the hosts to some extent. Thus *E. nycticebi*, which appears to be the most primitive parasite occurs in lorises (Fig. 14, j) and has the most strongly divided spicule; *E. lemuris* (k), although with a shortened male tail, possesses a spicule which is almost, although not quite, as strongly divided as that in the previous species (personal observation, Fig. 11), and occurs in lemurs. Above this level there is a great reduction in the extent of the division of the spicule which it is difficult to interpret since I have only Sandosham's figures which have not all been drawn from the same angle so that their comparison is difficult. It is clear that the spicule of *E. lerouxi* shows no indication of a division into two, while the spicule of *E. vermicularis*—which I have studied—is also not divided. The first species occurs in the gorilla and the second in Man. Between these extremes are *E. bipapillatus* (l) and *E. brevicauda* (m) in both of which the division of the spicule has been reduced. It is difficult to decide on the relative status of these two species since it is impossible to know whether the apparent differences between them are due to the angle from which the spicules were studied or are due to some structural difference. If the differences suggested by Sandosham's figures exist *brevicauda* appears to be more advanced than *bipapillatus* with the reduction of only one wing of the basal portion. This asymmetrical reduction appears to have reached a climax in *E. anthropopitheci* (o) in which there appears to be a complete loss of one half of the basal portion of the spicule with a great reduction in the remaining half. The last species—*E. buckleyi*—from the orang utan, has well defined double wings at the anterior end but they appear to represent a secondary modification since they are figured by Sandosham as lying along the longitudinal axis of the spicule and not projecting laterally from it as in the other " doubled " spicules.* This trend certainly shows some correspondence with the phylogeny of the hosts but the relationships between the species are clearly not linear. Thus forms ' l ', ' m ' and ' o ' appear to represent a trend towards singleness by the reduction and loss of only one side of the anterior ends while ' p ' appears to have arisen by the reduction and concomitant fusion of both sides.

The species occurring in rodents have not been considered above and have not been included in the figure (Fig. 14). They both represent fairly generalized forms without any definite morphological specialization. To this extent they could be interpreted as morphologically primitive (see Fig. 7, head of *T. sciuri* and Fig. 10, tail of *E. parallela*). This does not necessarily indicate that they represent descendants of the same parasite stock which was present in the primitive mammalian stock from which the rodent and primate lines diverged. They may, and I think more probably do, represent a transfer of an *Enterobius* and *Trypanoxyuris* form from the primate to the rodent lines owing to the ecological similarities of the two groups.

* The position of *E. zakiri* cannot be determined because of the poor description given by Siddiqi & Mirza (1956) which is insufficient by modern standards.

Cameron (1929), after considering all the then known species of *Enterobius*, put forward two suggestions: (1) " . . . one species (of *Enterobius*) restricts itself to one genus of host . . . " and (2) that it appeared possible to arrange the species in a series such that the hosts most closely related to Man had the parasites which were most similar to the species occurring in Man, i.e. that the phylogeny of the parasites parallels that of the hosts. Sandosham (1950) considered the questions anew and, after rightly pointing out that Cameron did not specify the characters on which his second suggestion was based concluded " . . . none of the characters of the parasites show a gradation in correspondence with the evolutionary position of the host " and also that the evidence did not support Cameron's first suggestion. The tendency for one species of parasite to be restricted to one genus of host is certainly clear but the " rule " has broken down in the cases of *E. vermicularis* occurring in a chimpanzee, a Lion marmoset and in a Lar gibbon at the Zoological Gardens, London (Sandosham 1950)—there is no reason to suppose that Sandosham misidentified his material. Similarly Inglis & Díaz-Ungría (1960) recorded *T. trypanurus* from *Chiropotes chiropotes* while Vevers (1923) described it from *Pithecia monachus*, in the Zoological Gardens, London and *T. interlabiata* from *Cebus nigrivittatus* reported by Sandosham from *Aotus felinus* also in the London Zoo. It should be noted that all the atypical records are from hosts in captivity. The only large number of parasites taken from hosts in the wild is that reported on by Inglis & Díaz-Ungría (1960) and in that case the rule applied without exception (there is some doubt about the host identification in the apparent exception, *T. interlabiata* from *Chiropotes satanas*). They reported eight samples from *Chiropotes chiropotes*, all *T. trypanoxyuris* ; one sample from *Ateles* sp., *T. atelis* which has been recorded from three, perhaps four, species of the same genus; and nineteen samples of *T. minutus*, all from *Alouatta* species. It is reasonable to conclude that " Cameron's Hypothesis " —one species of parasite: one genus of host—is a good general guide to the conditions which are likely to be found in the wild. This does not necessarily imply that there is host specificity in the sense that the parasites can only exist in hosts of one genus since the apparent restriction in distribution may be due to ecological factors. Thus the parasites might be able to infect hosts of other genera if the opportunity arose, a qualification supported by the cases referred to above of species being recovered from " atypical " hosts. The second suggestion put forward also seems to be, at least in part, correct since, as is pointed out above, in the genus *Enterobius* there is some tendency for the species with the more " advanced "—i.e. more fused—spicules to occur in the most advanced primates. However it has been stressed above, and is stressed again here, that the only conclusion that can be reached within both *Enterobius* and *Trypanoxyuris*, from the evidence at present available is that certain morphological trends exist, trends which may, but do not necessarily correspond to a phylogeny. The whole complex of species considered above cannot be fully analyzed until more information is available on the host distribution of the parasites, and the suggestions set out must be considered tentative.

The paucity of our information on the distribution of the parasites is easily illustrated by listing the genera included by Simpson (1945) in the suborder

Anthropoidea and noting from which of them species of *Enterobius* or *Trypanoxyuris* have been recorded. Simpson includes fourteen genera of living monkeys in the superfamily Ceboidea, from twelve of which nematodes have been recorded, but from only ten of which are species of *Trypanoxyuris* known, thus : *Allouata*, *Aotus*, *Ateles*, *Brachyteles*, *Callithrix*, *Chiropotes*, *Lagothrix*, *Pithecus* and *Saimiri*; nematodes other than *Trypanoxyuris* have been reported from the following four genera: *Cacajao*, *Callicebus*, *Cebus* and *Leontocebus* (*E. vermicularis* in the Zoological Gardens, London) ; no nematodes have been reported from the following genus : *Callimico*. In the superfamilies Cercopithecoidea and Hominoidea Simpson lists twenty-one genera—plus *Homo*—from sixteen of which nematodes have been recorded, but species of *Enterobius* are known from only eight, thus: *Cercopithecus*, *Colobus* (but only as *Enterobius* sp.—in Africa—Strong and Shattuck, 1930), *Gorilla*, *Macaca**, *Pan*, *Papio*, *Pongo* and *Presbytis;* nematodes other than *Enterobius* have been recorded from the following eight genera: *Cercocebus*, *Cynopithecus*, *Erythrocebus*, *Hylobates* (*E. vermicularis* in London Zoo), *Mandrillus*, *Nasalis* (only one report of a nematode of any kind), *Symphalangus* and *Theropithecus* (one record of a nematode); no nematodes have been recorded from the following five genera: *Allenopithecus*, *Comopithecus*, *Pygathrix*, *Rhinocephalus* and *Simia*.

It might appear from the lists of Old World genera that species of *Enterobius* tend to be restricted to members of the Hominoidea since all but one of the genera of that superfamily are known to be hosts to species of *Enterobius*, which are, on the other hand, known from only three genera of the Cercopithecoidea. It is fairly certain that this apparent bias is accidental and due to sampling since the records from the Hominoidea are almost all due to Sandosham (1950) and it is probable that an equally careful examination of the Cercopithecoidea would lead to the discovery of many further species of *Enterobius* and establish a much wider host range for the genus.

RELATIONSHIPS OF *ENTEROBIUS* AND *TRYPANOXYURIS*

Any attempt to determine the relationships of the genera *Enterobius* and *Trypanoxyuris* must involve a consideration of the entire family Oxyuridae. The classification given by Chabaud (1957) forms a convenient point from which to start such a discussion since he has satisfactorily brought together all the apparently related genera which were split up into many families and subfamilies by Skrjabin & Schikhobalova (1951). Chabaud divided the family Oxyuridae into two subfamilies Oxyurinae and Pharyngodoninae, but the first of these contains two distinct groups which can be distinguished very easily by the form of the male tail and to lump them together appears excessive —I have discussed this with Chabaud and he agrees. One of the groups is characterized by the male having a long tail with smallish, sessile papillae grouped around the cloacal opening, caudal alae which are relatively narrow and are not supported by papillae, a tendency for the cephalic region of the

* Bezubir and Furmaga (1959) record one female specimen, which they refer to *Trypanoxyuris* (=*Enterobius*) *bipapillata*, from *Macaca rhesus* in China. The status of this specimen cannot be established but it is almost certainly not referable to *E. bipapillata*. It is possibly a previously undescribed species.

body to develop cuticular excrescences of various kinds, (*Aspiculuris*, *Cephaluris*, *Heteroxynema* and *Labiostomum*), for the posterior end of the male to develop ridges or suckers anterior to the cloacal opening, (*Cephaluris*, *Dermatoxys*, *Dermatopallarya*, *Heteroxynema* and *Labiostomum*), and for the spicule to be lost. A short spicule has been described from *Dentostomella* and from *Dermatoxys veligera* (Rudolphi, 1819), *D. getula* Seurat, 1915 and *D. romerolagi* Bravo Hollis, 1950 while no spicule has been found in *D. ruficaudata* Mirza, 1936 and *D. vlakhaasi* (Ortlepp, 1937); no spicule has been reported from *Aspiculuris*, (?) *Dermatopallarya*, *Heteroxynema* and *Labiostomum*; a very small spicule has been described from *Cephaluris ochotonae* Akhtar, 1947 and *C. coloradensis* Olsen, 1949 but from none of the other species of the genus and I have elsewhere (Inglis, 1959b) considered it doubtful whether any species of the genus actually has a spicule; the same doubt can be expressed about the spiculate forms of *Dermatoxys*. The other group of genera, which includes *Enterobius* and *Trypanoxyuris*, is characterized by a short male tail with very broad caudal alae supported by long papillae and by very little elaboration of the cephalic region of the body.

With the exception of *Dentostomella* the male tales of the genera in the first group are virtually identical and the genera form a very uniform morphological group which it is reasonable to interpret as natural. Whether or not the second group can be considered a natural assemblage is more difficult to decide. The male tails are similar but show more diversity of structure than those of the first group, although there appears to be more constancy in the form of the mouth opening and the structure of the head. In spite of this uncertainty it is better to group all these genera together and I propose that the two groups should be treated as tribes of the subfamily Oxyurinae. Whether or not the groups so formed are related to each other cannot be decided on the basis of the evidence available since it is impossible to know whether they have been derived from the genera grouped in the subfamily Pharyngodoninae or not, mainly because of our lack of information on that subfamily. Thus, *Tachygonetria*, for example, contains a very diverse group of species the interrelationships of which cannot be unravelled until the structure of the head has been studied in detail. Similarly the genus *Pharyngodon* appears to show a greater range of variation in the structure of the head than has been appreciated heretofore (see Chabaud & Golvan, 1957). The consideration of this genus is further complicated by the various descriptions of the posterior end of the male from which it is clear that what has been referred to as a spicule is in many cases the modified posterior lip of the cloacal opening. This modification appears to be homologous with the gubernaculum-like structure occuring in genera such as *Alaeuris*, *Mehdiella*, *Ozolaimus*, *Tachygonetria* and *Veversia*.

I therefore propose that the subfamily Oxyurinae be subdivided as follows:

Subfamily **OXYURINAE** (Cobbold, 1864)

Oxyuridae: oesophagus relatively short; excretory system not prominent; gubernaculum, when present, never supporting posterior lip of cloacal opening. Parasites of warm-blooded vertebrates.

Type genus: *Oxyuris* Rudolphi, 1803.
Distribution: Cosmopolitan.

Tribe OXYURINI

Oxyurinae: little elaboration of anterior end of body; male tail short with broad alae supported by long narrow papillae; spicule always present.

The following genera are referred to this tribe:
Oxyuris Rudolphi, 1803; *Auchenocantha* Baylis, 1929 (this genus is probably indistinguishable from *Citellina*. =*Hoepplius* Chu, 1931 (Chabaud, 1957)); *Austroxyuris* Johnston and Mawson, 1938; (?) *Carolodelatorrella* Vigueras, 1943; *Citellina* Prendel, 1928; *Enterobius* Leach, 1953; *Helminthoxys* Freitas, Lent and Almeida, 1937, *Hoplodontophorus* Turner, 1921 (The only species referred to his genus, *H. flagellum* (Hemprich and Ehrenberg, 1828), is spectacular in the highly modified oesophagus and the large sucker on the male tail. In spite of its peculiarities it is clearly related to the other genera referred to in this tribe and there are insufficient reasons to separate it from them (see Inglis, 1959a); *Passalurus* Dujardin, 1845; *Protozoophaga* Travassos, 1923; *Skrjabinema* Werestchajin, 1926; *Syphacia* Seurat, 1916; *Syphaciuris* Skrjabin and Schikhobalova, 1951; *Trypanoxyuris* Vevers, 1923; *Wellcomia* Sambon, 1907 (=*Evaginuris* Skrjabin and Schikhobalova, 1951 (Chabaud, 1957)).

Tribe HETEROXYNEMATINI

Oxyurinae; elaboration of anterior end of body common; male tail long with narrow alae not supported by papillae; caudal papillae sessile, grouped around cloacal opening; spicule frequently lost; pre-cloacal elaboration frequently takes form of a cuticular fringe; oesophagus frequently without posterior tri-valvulate bulb.

The following genera are referred to this tribe:
Heteroxynema Hall, 1916; *Aspiculuris* Schulz, 1924; **Cephaluris* Akhtar, 1947; *Dentostomella* Schulz and Krepkogorskaja, 1932; *Dermatopallarya* Skrjabin, 1924; *Dermatoxys* Schneider, 1866; *Labiostomum* Akhtar, 1941 (=*Eugenuris* Schulz, 1948 (Inglis, 1959)); *Smirnovia* Schulz and Andrejeva, 1950 (This genus may be indistinguishable from *Labiostomum*); *Syphaciella* Mönnig, 1924 (This genus occurs in birds and is morphologically atypical in having two spicules. The form of the male tail and the distribution of the caudal papillae, however, is so very similar to that characteristic of the other genera of this tribe that the only course is to classify it with them); (?) *Acanthoxyuris* Sandground, 1928 (The systematic position of this genus is not clear since no males have been described. It is referred to this tribe, provisionally, because of the elaboration of the cephalic region of the body).

THE SYSTEMATIC POSITION OF *CALLISTOURA BRYGOOI*

Chabaud & Petter (1958) described *Callistoura brygooi* from a *Lemur macaco* in Madagascar. In discussing its affinities they considered it to approach

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Oxyuris most closely, but it differed from that genus so markedly that they created the genus *Callistoura* for its reception. They considered their species to approach *Oxyuris* most closely in the form of the oesophagus and the structure of the male tail; but, although the oesophagus is certainly similar to that in *Oxyuris*, it is also similar to that in *Hoplodontophorus*. The same shortening and loss of valves in the posterior bulb is apparent although in *C. brygooi* there is no indication for a long oesophagus with a distinct trivalvulate posterior bulb in the larva as in *Hoplodontophorus* (see Dollfus & Monod, 1933). This shortening and modification of the oesophagus does not necessarily indicate any close relationship between the genera in question since it is possible that it has appeared independently in highly evolved genera such as these. On the other hand, while *Oxyuris* and *Hoplodontophorus* are very similar in the structure of the male tail, in spite of the elaboration of a precloacal sucker in the latter genus, *Callistoura* is different from them both. This difference is particularly startling in the structure described by Chabaud & Petter as a spicule. The structure in question is single and, as Chabaud & Petter point out, supports the genital cone. Through the courtesy of Professor Chabaud I have been able to study specimens of *C. brygooi* and the structure is the same as that described by Inglis, Díaz-Ungría & Coles (1960), in *Ozolaimus*, as a gubernaculum. I refer specifically to *Ozolaimus* because I have studied that genus in detail although it is clear from published descriptions that such a structure is also found in several other genera (see above, page 117). I have been unable to find any trace of a spicule in *Callistoura*.

The similarity between *Callistoura* and the *Ozolaimus* group of genera is also marked in the arrangement of the caudal papillae on the male tail. Thus the structures referred to by Chabaud & Petter as " lames ventro-laterals " are highly modified papillae of the type so characteristic of *Ozolaimus* while the " lames laterales " of the genital cone are probably comparable to the thin cuticular structures with digitiform processes found in *Ozolaimus* between the most anterior pair of papillae and the anterior lip of the cloacal opening. The other structures surrounding the cloacal opening in *Callistoura* do not appear to have any direct equivalent in *Ozolaimus* although it is possible that the " digitation antérieure " is comparable to the digitiform processes referred to above in *Ozolaimus*.

These characters suggest that *Callistoura* originated from some pharyngodonin stock within Madagascar independently from all the other oxyurid genera occuring in warm-blooded hosts. This accords with the isolated position of Madagascar which has already been so clearly established by Professor Chabaud in much of his work. The loss of the spicule in *C. brygooi* with the retention of the genital cone with its cuticular support parallels the similar condition found in some species of *Pharyngodon* (see page 117) but does not necessarily indicate that the two genera are closely related. The detailed structure of the male tail does not support such a hypothesis and I consider it more probable that the same tendency towards the loss of the spicule has found expression independently in the two genera. The systematic relationships of *Callistoura*, although clear in broad outline, cannot be established in detail until a full study of the Pharyngodoninae can be undertaken and I suggest that

Type genus: *Oxyuris* Rudolphi, 1803.
Distribution: Cosmopolitan.

Tribe OXYURINI

Oxyurinae: little elaboration of anterior end of body; male tail short with broad alae supported by long narrow papillae; spicule always present.

The following genera are referred to this tribe:
Oxyuris Rudolphi, 1803; *Auchenocantha* Baylis, 1929 (this genus is probably indistinguishable from *Citellina*. =*Hoepplius* Chu, 1931 (Chabaud, 1957)); *Austroxyuris* Johnston and Mawson, 1938; (?) *Carolodelatorrella* Vigueras, 1943; *Citellina* Prendel, 1928; *Enterobius* Leach, 1953; *Helminthoxys* Freitas, Lent and Almeida, 1937, *Hoplodontophorus* Turner, 1921 (The only species referred to his genus, *H. flagellum* (Hemprich and Ehrenberg, 1828), is spectacular in the highly modified oesophagus and the large sucker on the male tail. In spite of its peculiarities it is clearly related to the other genera referred to in this tribe and there are insufficient reasons to separate it from them (see Inglis, 1959a); *Passalurus* Dujardin, 1845; *Protozoophaga* Travassos, 1923; *Skrjabinema* Werestchajin, 1926; *Syphacia* Seurat, 1916; *Syphaciuris* Skrjabin and Schikhobalova, 1951; *Trypanoxyuris* Vevers, 1923; *Wellcomia* Sambon, 1907 (=*Evaginuris* Skrjabin and Schikhobalova, 1951 (Chabaud, 1957)).

Tribe HETEROXYNEMATINI

Oxyurinae; elaboration of anterior end of body common; male tail long with narrow alae not supported by papillae; caudal papillae sessile, grouped around cloacal opening; spicule frequently lost; pre-cloacal elaboration frequently takes form of a cuticular fringe; oesophagus frequently without posterior tri-valvulate bulb.

The following genera are referred to this tribe:
Heteroxynema Hall, 1916; *Aspiculuris* Schulz, 1924; **Cephaluris* Akhtar, 1947; *Dentostomella* Schulz and Krepkogorskaja, 1932; *Dermatopallarya* Skrjabin, 1924; *Dermatoxys* Schneider, 1866; *Labiostomum* Akhtar, 1941 (=*Eugenuris* Schulz, 1948 (Inglis, 1959)); *Smirnovia* Schulz and Andrejeva, 1950 (This genus may be indistinguishable from *Labiostomum*); *Syphaciella* Mönnig, 1924 (This genus occurs in birds and is morphologically atypical in having two spicules. The form of the male tail and the distribution of the caudal papillae, however, is so very similar to that characteristic of the other genera of this tribe that the only course is to classify it with them); (?) *Acanthoxyuris* Sandground, 1928 (The systematic position of this genus is not clear since no males have been described. It is referred to this tribe, provisionally, because of the elaboration of the cephalic region of the body).

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it be treated provisionally as a genus *incertae sedis*, closely related to the subfamily Pharyngodoninae.

ACKNOWLEDGMENTS

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AN EXPERIMENTAL STUDY OF THE INTERNAL RHYTHM OF REPRODUCTION IN THE RED-BILLED DIOCH *QUELEA QUELEA* BY MEANS OF PHOTOSTIMULATION, WITH A NOTE ON MELANISM INDUCED IN CAPTIVITY

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(With 1 plate)

The cyclical testicular events in the tropical weaver-finch *Quelea quelea* are basically the same as those of temperate zone species but are modified for a xerophilous mode of life. Photostimulation is not necessary for the development of the sexual cycle and immediately the abbreviated regeneration period is over *Q. quelea* will again achieve spermatogenesis under an unchanging 12 hr. 25 min. daylength. An abnormally long photoperiod of 17 hrs. influences gonad growth during the pre-nuptial acceleration phase and causes premature metamorphosis. It has no influence, however, on the duration of the regeneration phase. Some *Q. quelea* maintained in captivity develop a black plumage. This induced melanism is briefly reported.

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INTRODUCTION

It has been previously shown that the nomadic xerophilous dioch (*Quelea quelea*) a trophical bird that lives on both sides of the equator, has a sexual cycle that is susceptible to experimental stimulation by light even though photostimulation cannot be a regulatory factor in its breeding season (Marshall & Disney, 1956). Recently, Disney, Lofts & Marshall (1959) have used this capacity for photostimulation to show that there exists in this species the post-nuptial period of sexual regeneration (and negativity) characteristic of wild birds. However, in *Q. quelea* which breeds only after heavy rain falls and irrespective of the cycle of the sun, this period lasts a mere six weeks.

In many temperature zone species it may persist for a period of up to four months. Disney *et al.* (1959) further showed that after this abbreviated period of post-nuptial regeneration, the gonads of *Q. quelea* begin to grow whether the birds are kept under an artificial equatorial daylength of 12 hours or under a 17 hour daylength.

Wolfson & Winchester (1959) has written as follows: "If day length conditions govern the duration of gonadal activity in the Tropics, as they appear to do in the North Temperature latitudes, then day length would play a primary role in determining the time of breeding in the tropics. Such a role would be critical if a preparatory (i.e. regeneration) phase existed, and if the duration of the preparatory phase was also a function of day length. . . . . Additional studies . . . . are expected to yield information bearing on the preparatory phase of the gonadal cycle."

From past, and presently reported evidence, we believe that 1. *Q. quelea* has in fact a preparatory (= post-nuptial regeneration) phase and 2. that the duration of this phase is in this tropical bird independent of photostimulation.

MATERIALS AND METHODS

Quelea quelea is dimorphic, the male periodically assuming vivid nuptial plumage. The birds used were collected in Tanganyika (lat. 6° 11′ S) where immense flocks oscillate back and forth across the equator according to the food supply. Here the main breeding period is in April after the more or less regular rains (Disney & Marshall, 1956) but reproduction can occur at other times. After reproduction the males moult into non-breeding plumage and become indistinguishable from the permanently sombre females. Specimens were collected in June and sent to London by air where they were established in a colony at St. Bartholomew's Hospital Medical College and left for two weeks to settle down at a temperature of about 75° F under a 12 hour daylength.

The experiment was begun on 13th August as follows :

Group 1. Twenty males and ten females were killed. Their gonads were dissected out for histological examination and a record was made of plumage condition.

Group 2. Ten males and ten females were placed under a photoperiod of 12 hours 25 mins. the daylength at that time of the year in the area from which they came.

Group 3. Eleven males and ten females were placed under a photoperiod of 17 hours that is known to be stimulatory to the species (Marshall & Disney, 1956).

The birds in the two last-mentioned groups were first laparotomized under open ether anaesthesia and the size of the left testis measured *in situ*. Closure was effected by a single suture and in each case the wound healed uneventfully within a few days. Later, during the period 2nd October to 4th October, the photostimulated males were unilaterally castrated ; the left testis was removed for histological examination. At the same time half the number of female specimens were killed for histological investigation of the ovary. The experiment was terminated on 28th November when all remaining specimens were killed and the gonads preserved for internal examination.

Gonadal material was subjected to the same procedures as follows : After measurement of the whole testis a portion was fixed in formal-calcium solution for subsequent gelatine embedding. The remainder was fixed in Bouin's fluid and embedded in wax. Gelatine-embedded material was sectioned on a freezing microtome at a thickness of 8μ and coloured with Sudan black for the revelation of lipoidal material. Wax sections were cut at 6μ and stained with iron haematoxylin and orange G for the determination of the gametogenetic condition.

A colateral experiment has been briefly reported elsewhere (Disney *et al.*, 1959) and the results summarised in Table 3 below.

RESULTS

Group 1 : The males fell into three sub-groups as follows :

(*a*) Juveniles (five specimens). These retained the neutral plumage, a very dark brown iris and a dark eye-ring. Skulls were still only partly ossified. The testes were minute (less than 1mm. in diameter) and the tubules were only 20 to 30μ in diameter and contained merely a single peripheral layer of spermatogonia. Interstitial tissue was extensive and many of the Leydig cells held dense, cholesterol-positive lipoidal material. The tubules contained no lipids.

(*b*) Adults passing into breeding plumage (ten specimens). Crown feathers were still neutral in type but the black nuptial face mask was beginning to appear. Testes had grown to between 3×2 mm. and $4 \times 2{\cdot}5$ mm. and tubules were now from 75 to 130μ in diameter. Some primary spermatocytes had arisen. These adults had already been through a breeding season ; within the tubules there remained sudanophil material, the remnants of the previous season's post-nuptial tubule steatogenesis. Interstitial Leydig cells had become moderately lipoidal and chloesterol-positive.

(c) Adult males in full nuptial plumage (five specimens). These birds had been artificially stimulated in an experiment in Africa before their despatch and now displayed complete breeding plumage of black facial mask and pale straw-coloured crown and breast feathers. The testes had now reached maximum size (about 10×6 mm.) and the tubules had swollen to a diameter of 250 to 350μ and were full of bunched spermatozoa. The Leydig cells had discharged their lipids.

Female birds (ten specimens) of Group 1 remained in the eclipse condition with neutral plumage and red bills. (During the breeding season the bills become bright yellow, but the plumage remains sombre.) The largest oocytes measured 500μ in diameter with the exception of those of one female (probably a juvenile) in which the largest was only 175μ in diameter.

Group 2 : Table 1 summarizes the changes that occurred in the males retained under the Tanganyika day-length of 12 hours 25 mins. By 3rd October eight out of the ten specimens had assumed full nuptial plumage and their testes had reached the maximum size with tubules full of spermatozoa and interstitial cells exhausted of lipids. The two juveniles, however, were still in neutral plumage and possessed inactive gonads. (One of these unfortunately died during an operation). At the end of the experiment the remaining

juvenile was starting to assume nuptial plumage and spermatogenesis had begun. With the exception of specimen No. 7 adult birds were histologically and morphologically unchanged from the condition recorded at the time of unilateral castration. In the exceptional individual the remaining testis was undergoing the first stages of tubule steatogenesis and has been placed in a separate category (d).

Table 1—Testis size (in mm.) and breeding condition of *Quelea* kept under a Tanganyika photoperiod of 12 hours 25 minutes.

Specimen no.	Date August 13th	October 3rd	November 28th
1	minute (a)	minute (a)	—
2	minute (a)	minute (a)	5×3 (b)
3	4×2·5 (b)	10×6 (c)	10×6 (c)
4	4×3 (b)	10×6 (c)	9×8 (c)
5	3×3 (b)	10×6 (c)	9×8 (c)
6	4×3 (b)	10×6 (c)	10×6 (c)
7	8×7 (c)	10×7 (c)	7×6 (d)
8	9×6 (c)	10·5×7 (c)	10×6 (c)
9	10×6 (c)	10×6 (c)	9·5×8 (c)
10	10×6 (c)	10×6 (c)	10×6 (c)

(a) = Juvenile.
(b) = Adult entering nuptial plumage.
(c) = Adult in full nuptial plumage.
(d) = Post-nuptial testis metamorphosis has begun.

The five females killed at the time of castration had red beaks and the average size of the largest oocytes was 350μ. By 28th November the beaks had become bright yellow (except at the extreme tip) and oocytes had increased to 650μ, and in one case 1·1 mm., in diameter.

Group 3 : The results are summarized in Table 2. At the time of the initial laparotomy one male specimen (No. 11) was still in eclipse plumage and superficially resembled a juvenile. Testis autopsy on 3rd October revealed tubules that had already undergone spermatogenesis and subsequent post-nuptial metamorphosis. The abnormally long (17 hour) photoperiod produced an acceleration of the cyclical events in the gonads of all specimens. By the time the experiment ended on 28th November the juveniles had attained full breeding condition, as had also the adult previously in eclipse. The majority of the remainder (nos. 4, 5, 9 and 10) were undergoing post-nuptial gonadal metamorphosis. Specimens 9 and 10 had reached the last stages of tubular steatogenesis and possessed collapsed seminiferous tubules (shrunk to a diameter of only 36 to 50μ) filled with a dense amorphous mass of cholesterol-positive lipid. Interstitial rehabilitation had begun and juvenile Leydig cells contained a scattering of small sudanophil droplets in the cytoplasm. Still in full nuptial plumage, these two specimens were starting their post-nuptial moult.

On 3rd October all females were in a uniform condition with red beaks. Those killed for autopsy (four specimens) possessed oocytes measuring up to 450μ in diameter. By 28th November four specimens possess yellow beaks

Table 2.—Testis size (in mm.) and breeding condition of *Quelea* kept under a 17 hour photoperiod.

Specimen no.	Date August 13th	October 4th	November 28th
1	minute (a)	minute (a)	10×7 (e)
2	minute (a)	minute (a)	9×4·5 (e)
3	minute (a)	minute (a)	—
4	4×3 (b)	10×5 (e)	5×3 (d)
5	4×2·5 (b)	10×6·5 (e)	6×4 (d)
6	2·5×2 (b)	6×3 (e)	10×6 (e)
7	3·5×2 (b)	8×4·5 (e)	10×6 (e)
8	3×2·5 (b)	3×2·5 (b)	—
9	10×6 (e)	6×4 (d)	2×1 (e)
10	6×6·8 (e)	6×3·5 (d)	2×1 (e)
11	2×1 (f)	3×2 (b)	8×5 (e)

(a) = Juvenile.
(b) = Adult entering nuptial plumage.
(c) = Adult in full nuptial plumage.
(d) = Post-nuptial testis metamorphosis has begun.
(e) = Testis at height of steatogenesis and post-nuptial moult has started.
(f) = Adult in eclipse plumage.

and oocytes expanded to between 800 and 1000μ in diameter. The beaks of the remaining two, however, had become yellow only at the edges and the largest ovarian oocytes did not exceed 500μ in diameter. Judged by skull condition and eye-ring colour these were probably juveniles.

DISCUSSION

The results reaffirm that the cyclical testicular events in the tropical weaver-finch *Quelea quelea* are basically the same as those of temperate zone species. They are, however, modified to suit its xerophilous mode of existence. Periods of regeneration, acceleration and culmination occur in both regions, but in the *duration* of the regenerative phase there is a marked difference. In temperature zone species this phase (during which gametogenesis cannot occur) lasts some four months and ensures that reproduction will not occur during the late summer and autumn. In *Q. quelea*, on the other hand the period of sexual negativity lasts for only a few weeks and so the species can take advantage of good conditions for breeding at any time that rain falls in its generally arid environment.

It will be seen from our results that immediately the brief regeneration period is over *Q. quelea*, when given adequate light and food, will achieve spermatogenesis under an unchanging 12 hour 25 min. daylength (Table 3). Like the xerophilous Australian budgerygahs (*Melopsittacus undulatus*) (Vaugien, 1952, 1953) and zebra finch (*Poephila castenotis*) (Marshall & Serventy, 1958) it does not require photostimulation for the development of its sexual cycle.

Nevertheless, our results make it clear that abnormally increased photoperiods of 17 hours daily (far longer than the species could receive in nature) influenced gonad growth during the pre-nuptial acceleration phase and caused premature metamorphosis (Table 2). Wolfson & Winchester (1959), on the other hand,

have reported that when they subjected three groups of *Quelea* in late November to 16·75, 12·75 8 hours daylength respectively maximum gonadal activity was attained in all groups by 31st January. Their 8 hour groups "regressed" (i.e. metamorphosed) whereas the groups under longer daylength apparently maintained testicular activity. It would be expected that the gonads of the two more intensely photostimulated groups would also have metamorphosed as did those of our comparably treated Group 3. We believe (see results embodied in Tables 2 and 3) that this in fact probably did occur in Wolfson's birds. It seems likely to us that Wolfson's 16·75 and 12·75 hour groups metamorphosed, went through their regeneration periods and once more achieved spermatogenesis during the two months between 30th January and 30th March. Such possible errors can be eliminated only by laparotomy and internal observation at regular intervals during each experiment.

Table 3—The effects of a 17 hour photoperiod on testis size (mm.) in *Quelea* at the height of spermatogenesis.

Specimen no.	Date			
	February 12th	March 5th	March 20th	April 6th
1	9×4·5 K	—	—	—
2	9×4	1×1 K	—	—
3	8×5·5	2×1·5 K	—	—
*4	10×5	1·5×1	1·5×1 L	7·5×5 K
*5	10·5×5	1·5×1·5	2×1·5	3×2 K
*6	10×5	2×1	6×4	7×6 K
*7	10×5	2×1·5	5×3 K	—
*8	10·5×6	1×1	2×1 L	8×5 K
9	9×4	2×1·5	2·5×1·5	3·5×2 K
10	9×5·5	1·5×1	4×3 L	7×3·5 K
11	9×4	1·5×1	3×2 L	5×2·5 K
12	10×5	1·5×1	1×1·5 L	2×1·5 K
13	10·5×6	1×1	1×1 L	2·5×2 K

* These specimens were placed under a 12 hour photoperiod from March 6th onward. All other specimens were maintained under a 17 hour photoperiod.

K = date on which specimen was killed.

L = specimen underwent unilateral castration and left testis removed.

Finally, we wish to record a remarkable plumage phenomenon seemingly induced by conditions of captivity. During the course of a year, about 8 per cent of the aviary stock developed black plumage (Plate 1). No less than forty-eight individuals of both sexes were affected. The appearance was noted during both eclipse and sexual periods. So far as we know, this is the only reported case of melanic *Q. quelea*. During the examination of many thousands of wild specimens in Tanganyika by one of us (H.J. de S.D.) melanism has not once been observed. This phenomenon is under investigation.

ACKNOWLEDGMENT

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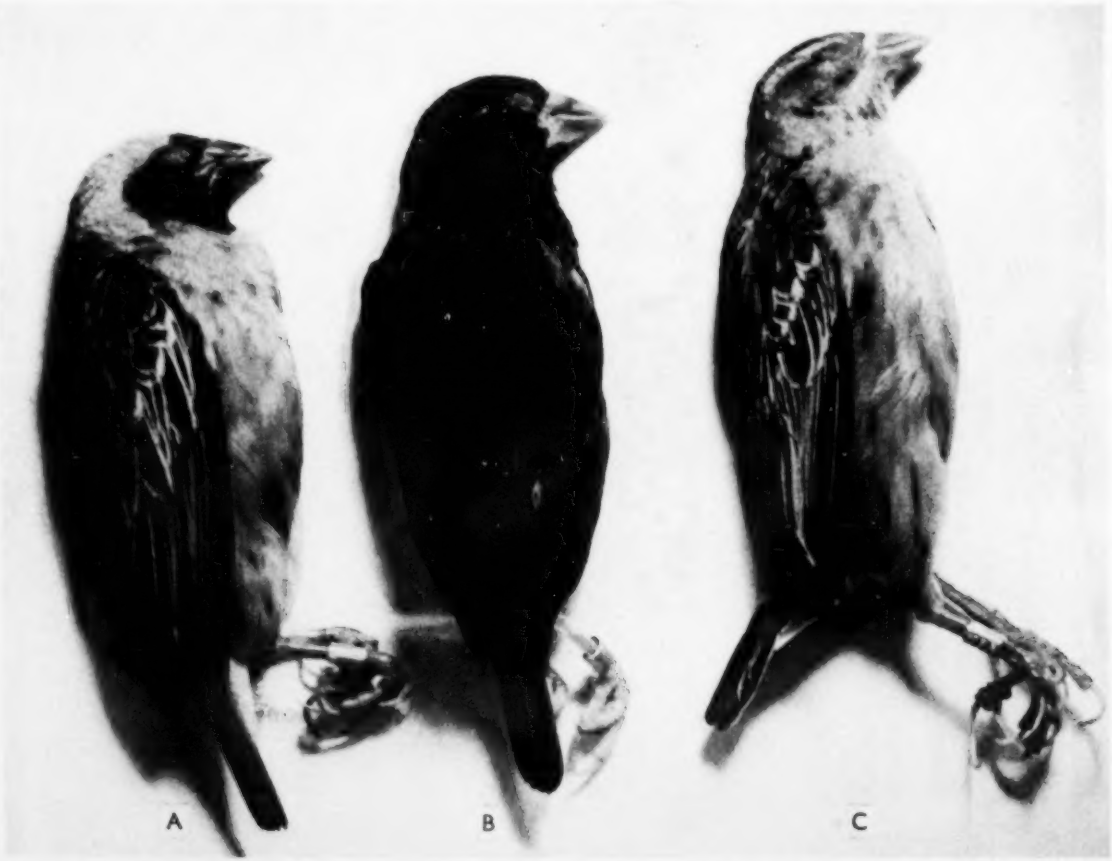

A. Male bird in full nuptial plumage. B. Female with melanic plumage. C. Female in normal breeding plumage.

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NOTES ON TOOTH REPLACEMENT IN THE NILE CROCODILE *CROCODILUS NILOTICUS*

BY

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(With 4 figures in the text)

The history and replacement of crocodile teeth are described. A new tooth erupts with only a short root which grows downwards into the socket as the pulp cavity in the crown begins to be occluded by the further deposition of dentine. After the root has become fully extended, it is gradually resorbed at its base to make room for an enlarging successional tooth which has been forming on the lingual side of the socket. The successional tooth eventually moves to a position within the partly resorbed functional root and directly under the functional crown. Progressive reduction of the functional root now occurs to accommodate the continuously enlarging successional tooth and, when resorption is largely complete, the functional tooth falls away, allowing the successional tooth, with a short, incomplete root, to take its place. As a result of this successional cycle it is found, within certain limits, that at any given time the form and condition of a functional tooth is related to the size and condition of its successor lying below.

Consideration of various measurements made on a series of twenty-four skulls of different sizes indicates that a regular and continuous replacement of teeth occurs throughout a large part of a crocodile's life. It is estimated that in a crocodile which is thirteen feet long, each tooth is likely to have been replaced forty-five times.

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INTRODUCTION

The general pattern of tooth replacement in crocodiles is well known (see Owen 1840–45, Mummery 1921) and, no doubt, throughout the ages speculation occurred repeatedly whenever the extraction of a functional tooth from a crocodile jaw revealed the presence of one or more immature teeth in the same socket. In the Nile crocodile, *Crocodilus niloticus*, it is usual to find one replacing tooth lying below a functional one, although two or even three replacing teeth may be present. It is on record that as many as six replacing teeth have been found in the same socket (Pitman, 1931). It is generally agreed that as an old tooth wears and finally falls away, it is replaced by the first successional tooth which has been formed in the socket below.

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A functional tooth has a long tubular root with a wide open base. A new tooth begins to form on the lingual side of the socket, but before formation is complete, the whole germ moves across until it lies directly under the functional tooth. The new tooth elongates, its tip moving up into the root of the functional tooth. Eventually, the new tooth erupts upwards along the axis of the old tooth to take up precisely the same position in the jaw. Histological accounts of this have been given by James & Wellings (1943) and, more recently, by Kvam (1958).

Estimates of the number of replacements occurring in each socket during the life of a crocodile vary considerably. It is commonly stated that there is a " continuous succession " of teeth; where authors have been more specific, estimates of the number of replacements vary from five (Röse, 1893) to twenty-five (Lison, 1954). As far as the whole tooth row is concerned, it is suggested that, as in many fossil reptiles, replacement in the crocodile occurs in antero-posterior waves (Romer, 1956).

This general view of tooth replacement in crocodiles has not gone unchallenged. Cawston (1945) believed that a tooth increased in size with age by means of a growth process in which the root slowly erupted and became invested with a coat of enamel. On such grounds it was argued that replacement would occur rarely, if at all. However, in view of the absence of any evidence for such a growth process, little support can be given to this theory.

A further description of crocodile teeth is given below, with the aim of adding more detail to the earlier accounts. In particular, it is shown how a tooth varies in form during its history and an attempt is made to arrive at a more concrete idea of the total number of replacements which might be expected during the life of a crocodile.

MATERIAL

The observations described were made on a series of twenty-four crocodiles (*Crocodilus niloticus*) collected from the shores of Lake Victoria near Jinja. The sizes of these animals varied from one and a half feet to 13 feet. After all the skin and flesh had been removed, each tooth row of each skull was examined in detail ; both functional teeth and successional teeth were removed and a number of measurements made, as follows:—

i. The length of the tooth row.

ii. The maximum, antero-posterior diameter of each tooth crown (see Fig. 1a, ' z ').

iii. The maximum, antero-posterior diameter of each first successional tooth in which formation of the crown had been completed.

The purpose of the first two measurements was to discover how, as a skull grows, an increase in the tooth size might be related to an increase in the length of the tooth row, and the purpose of the third measurement to determine the relative sizes of functional teeth and their successors. It will be seen later that only a few successional teeth in each tooth row are in precisely the right condition to enable a comparison with the functional tooth to be made.

Rather surprisingly, the difference in size between a functional tooth and its successor was so slight that it was necessary to make the measurements

with a micrometer screw gauge in order to appreciate the difference. In view of this it was felt necessary to check on the effects of drying on the tooth diameter. Some twenty teeth (i.e. ten functional and ten successional) were extracted from fresh skulls and measured; they were then dried and remeasured, and finally soaked in water and measured again. It was found that these drying and wetting processes had no effect on the dimensions of the crown.

Table I summarizes the various measurements for each skull.

VARIATION IN TOOTH FORM

In general, the crowns of all the teeth are pointed cones with rather flattened buccal and lingual surfaces, each of these surfaces having a number of vertical ridges running from the neck to the tip of the crown (Fig. 1a). The anterior and posterior sides are slightly more flattened to form cutting edges. The root is an elongated cylinder several times longer than the height of the crown, and the whole tooth is curved in the bucco-lingual plane so that the tips of the teeth tend to point inwards (Fig. 3).

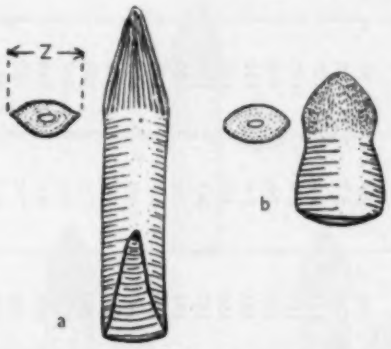

Fig. 1—Lingual view of two teeth of *Crocodilus niloticus*.
a. long, pointed tooth from anterior region of the jaw; the root is cylindrical and hollow, its length being more than twice the height of the crown; the latter has flattened cutting edges and vertical ridges converging towards the tip. A cross section of the tooth crown is illustrated to to the left, 'z' indicating the antero-posterior diameter.
b. short, squat tooth from the posterior end of the jaw; root somewhat flattened, its length not markedly greater than the height of the crown; the latter has no cutting edges and irregular ridges. A cross section of this tooth crown is also shown to the left.

However, there are differences in the crown shape and dimensions between teeth at the front and those at the back of the jaw (Fig. 1). The crown of a front tooth is long, gently tapering and markedly curved; the height of the crown is about twice the maximum diameter. From a point approximately halfway along the jaw to the hinder end, there is a gradual transition into a shorter, squat crown which is only slightly curved and whose height is only equal to the maximum diameter. The ridge patterns on these hind teeth are often weak and usually irregular.

Table 1

TOOTH ROW	Upper Left		Upper Right		Lower Left		Lower Right		
SKULL	Length of row	Mean tooth diameter	Length of row	Mean tooth diameter	Length of row	Mean tooth diameter	Length of row	Mean tooth diameter	Mean increase in diameter of replacing teeth*
A	35	1·0	35	1·0	25	1·0	25	1·0	not measurable
B	102	2·4	105	2·4	91	2·4	91	2·4	0·17 (10)
C	109	2·7	109	2·7	93	2·7	94	2·7	0·08 (3)
D	115	2·5	115	2·5	105	2·5	105	2·5	0·17 (6)
E	117	3·1	117	2·9	102	2·9	102	2·8	0·30 (1)
F	120	2·9	118	2·8	104	2·6	105	2·7	0·17 (7)
G	133	3·0	134	3·0	117	3·1	119	3·0	0·37 (8)
H	152	4·0	152	4·0	128	4·1	128	4·0	0·12 (10)
I	157	4·1	157	4·1	138	4·0	138	4·0	0·21 (9)
J	185	4·5	185	4·6	160	4·7	163	4·7	0·41 (15)
K	190	4·5	190	4·5	165	4·5	165	4·5	0·22 (8)
L	195	4·5	200	5·0	182	4·6	180	4·8	0·27 (8)
M	200	4·7	205	4·7	185	5·0	185	5·0	0·17 (11)
N	253	7·3	255	7·0	239	7·1	240	7·3	0·35 (7)
O	277	8·0	275	7·8	257	8·0	262	8·0	0·21 (9)
P	280	6·5	285	6·5	240	6·5	240	6·5	0·30 (12)
Q	285	7·5	282	7·5	257	7·3	255	7·3	0·35 (11)
R	290	8·2	290	8·3	260	8·0	260	8·0	0·32 (10)
S	315	9·0	320	9·0	280	9·0	280	9·1	0·16 (7)
T	325	8·5	330	8·5	288	7·6	288	7·9	0·40 (12)
U	340	8·7	343	8·7	..... Missing				0·19 (2)
V	345	8·6	347	8·8	305	8·5	300	8·5	0·20 (10)
W	350	9·0	350	9·0	300	9·0	300	9·0	0·25 (7)
X	470	13·0	470	13·0	385	12·0	385	12·0	0·28 (13)

Note a. All measurements are in millimetres.

b. *Figures in parentheses indicate the number of successional teeth in the whole skull from which this mean was calculated.

c. Some idea of the relative dimensions of these animals can be gained from the following, very approximate ratios

$$\frac{\text{Length of skull}}{\text{Length of body} + \text{tail}} \simeq \frac{1}{6{\cdot}5} \qquad \frac{\text{Length of lower tooth row}}{\text{Length of skull}} \simeq \frac{2}{3}$$

When the teeth are removed from their sockets, it is seen that variation occurs in the condition of roots of the functional teeth as well as in the crowns of the first successional teeth. Broadly speaking, a given functional root condition corresponds to a certain condition of the successional crown and it is evident from the examination of a series of jaws of different ages, that any functional tooth and its succesor in any position in a jaw could show any of the conditions illustrated in Fig. 2. This is because the different root and successional crown forms are really different stages in the history of the teeth. After consideration of these various tooth forms, the history of a tooth may be reconstructed.

On eruption, the crown of a new tooth is externally complete but the root is short ; it is likely that already at this stage the next successional tooth has started forming on the lingual side of the socket, although only the tip of the crown is present (Fig. 2a ; Fig. 3a). Having become fixed into the pre-existing socket, the root of the newly erupted tooth begins to extend downwards and growth continues until the final length is reached. The root is now a complete hollow cylinder (Fig. 2b ; Fig. 3b) and remains so for some time.

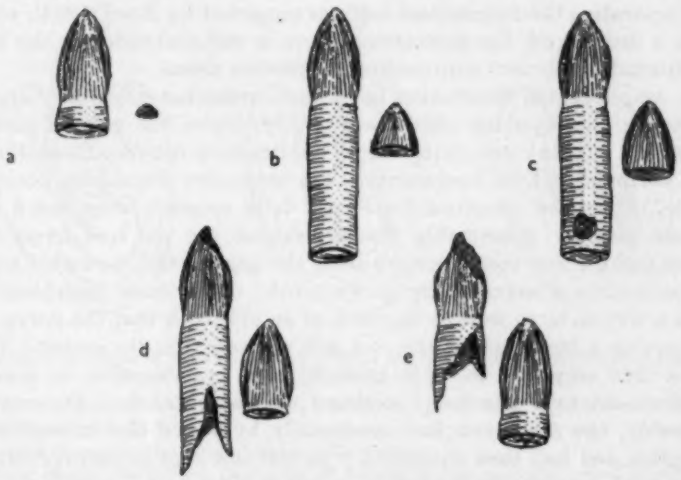

Fig. 2—The lingual appearance of various functional teeth, each accompanied by the first successional tooth.

a. Newly erupted tooth accompanied by only the tip of the crown of its successor.
b. Root of functional tooth fully elongated; crown of successor enlarged.
c. First stage of root resorption, crown of functional tooth showing first signs of wear.
d. Resorption of root proceeding, crown of successor complete.
e. Root resorption almost complete, crown badly worn; successional rooth in suitable condition for replacement.

But the successional tooth has continued to grow and, perhaps because of the increasing pressure exerted against it by the enlarging germ, the base of the functional root starts to be resorbed in order to make more space available. The first sign of this is a small hole on the lingual side of the root (Fig. 2c)

which enlarges into a space shaped like an inverted V (Fig. 2d ; Fig. 3c). More and more of the lingual surface is resorbed and eventually the whole of the successional germ moves through the resorption gap to take up a position within the root and directly below the crown of the functional tooth. As yet the crown of the successional tooth is not complete and although its change in position is no doubt partly due to the fact that it is too large to remain in the original place, the movement may also be required because of the appearance at about this stage of the second successional germ (Fig. 3d). As these changes occur within the socket, the functional crown has been in use and shows increasing signs of wear.

Wholesale resorption of the root continues as the crown of the first successional tooth is completed (Fig. 2e), resorption of the lingual side always being in advance of that of the buccal side. With this resorption the tip of the successional tooth rises within the socket as a result of the growth below of the new root (Fig. 3e). The cycle is completed when resorption reaches the neck of the old tooth, the latter then being shed and replaced by its successor with a short root moving up along the same, original axis (Fig. 3f). In agreement with Kvam (1958), no evidence was found for the existence of bony alveoli separating the successional teeth as suggested by Röse (1893), although even in a dried skull, the successional germ is still embedded in the remains of its enamel organ and surrounding connective tissue.

The stages in the illustration have been somewhat arbitrarily chosen as representing those phases which most easily depict the general pattern of replacement. In any jaw, many stages intermediate between those illustrated are to be found, whilst irregularities and anomalies frequently occur. For example, on several occasions two teeth, fully erupted, were found sharing the same socket ; presumably this is because the old root never became resorbed and the new tooth grew up along the lingual side, the socket enlarging to accommodate a second, fully grown tooth. Sometimes, resorption occurs in such a way as to so weaken the neck of an old tooth that the crown breaks away leaving a large part of the root still embedded in the socket ; the new tooth is then only able to erupt partially. On one occasion, an unresorbed part of an old root was found enclosed within the root of the new tooth. Presumably, the new tooth had successfully by-passed the unresorbed piece on eruption and had then enveloped it as the new root extended downwards. There are other anomalies besides these, but in all cases it is possible to explain them as slight modifications of the general pattern, caused by an unusual circumstance. Thus, both normal and anomalous tooth conditions indicate that a tooth row is the site of continuous activity.

Once eruption has occurred, there is no change in the external form of the crown, except for wear and damage caused through use. Internally, however, changes do occur. At the time of eruption, the pulp cavity extends well up into the crown of the new tooth (Fig. 3a), which is, therefore, relatively hollow. But after eruption, this crown cavity is gradually occluded by the deposition of new dentine (Fig. 3b–f) so that the crown of a tooth gradually becomes a solid peg. Even in an old tooth, the original contour of the pulp cavity at eruption is often marked by a white line of atypical calcification, probably

due to a period of arrested development prior to eruption. It is of interest here that in some amphisbaenid lizards further deposition of dentine also occurs after the eruption of the tooth (Gans, 1957).

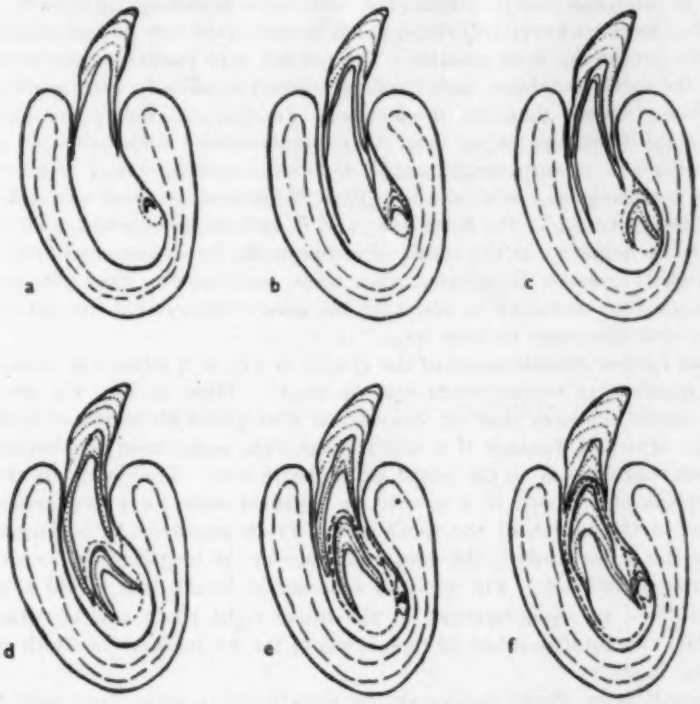

Fig. 3—A series of stages in the successional cycle as might be seen in transverse sections of a jaw.

a. Newly erupted tooth, with a short root, in position; germ of the successional tooth lying against the lingual wall of the socket.

b. Root of functional tooth extended deeply into socket.

c. Beginning of root resorption; deposition of dentine continuing inside crown of functional tooth.

d. Germ of first successional tooth has moved across to lie within the root of the functional tooth; functional crown largely occluded by dentine.

e. Large part of functional root resorbed; tip of first successional tooth moving upwards because of continued enlargement of the tooth; second successional germ makes its appearance.

f. Functional crown about to be shed; first successional tooth about to replace.

THE NUMBER OF REPLACEMENTS

In the series of skulls studied, it is seen (Table 1) that as the length of the tooth row increases, the mean width of the tooth crowns also increases. The precise relationship is more clearly seen if the figures are presented graphically (Fig. 4, A & B). From these graphs it is evident that a relatively close

relationship exists between the length of a tooth row and the mean width of the teeth in that row, or, as the tooth row increases in length, the amount of space occupied by tooth crowns along the row remains proportionally the same.

There are two ways in which this relationship could be maintained. One is that as the tooth row lengthens, the tooth crowns enlarge by growth ; this possibility has been previously disregarded in view of the fact that no mechanism exists for producing such growth. The second, and probable, mechanism is that as the tooth lengthens, each tooth is replaced repeatedly, each successional tooth being larger than its predecessor. In fact, as shown in Table I, successional teeth are larger than their predecessors, although the actual increase in size is surprisingly small (0·25 mm.—average) and is much the same in both large and small skulls. Thus, if the average tooth size is directly related to the length of the tooth row, and if an increase in average tooth size can only be achieved as the result of replacement by successional teeth with only slightly greater dimensions than their predecessors, then the number of replacements necessary to maintain the above relationship throughout the life of a crocodile must be very large.

After further consideration of the graphs in Fig. 3, a numerical estimate of of the numbers of replacements may be made. Thus, in Fig. 4A, the slope of the curve indicates that an increase in average tooth width of 0·25 mm. (i.e. the expected increase if a whole tooth row is replaced) corresponds to an increase of 8·0 mm. in the length of the tooth row. That is, on an average, one expects each tooth in a row to be replaced once for every increase of 8·0 mm. in the length of the tooth row. From smallest (A) to largest (X) skull in the series studied, the actual increase in the length of the lower right tooth row is 360 mm. For such an increase in length one would expect a total of $\frac{360}{8.0} = 45$ replacements. If the upper right tooth row is considered (Fig. 4B) the total number of replacements for an increase in tooth row of 435 mm. is 47.

It would seem, therefore, that during growth from a period soon after hatching to a body length of 13 feet, the set of teeth in each tooth row of a crocodile is likely to be replaced somewhere between 45 and 50 times, a figure considerably greater than the largest ever previously suggested. It must be admitted that the accuracy of this figure depends upon the figure for the average increase in size of a successional tooth over its predecessor. Moreover, this figure is the one most subject to error, in so far as relatively few of the first successional teeth are at the right stage in development to allow a size comparison to be made with the functional teeth. Nevertheless, even if the error is as great as 20 per cent, which is unlikely, the minimum number of replacements expected will still be as high as 40.

From the above account of tooth replacement in crocodiles, it would seem that the rate of replacement of teeth is directly related to the rate of growth of the jaw. In addition to his own observations, Cott (1960) has assembled such evidence as exists on the overall growth rates of crocodiles, from which it appears that during the first few years of life each individual increases in length by about 9·5 inches per annum. This growth rate drops to 1·5 inches per annum in later years and may be lower still in old animals. Really large

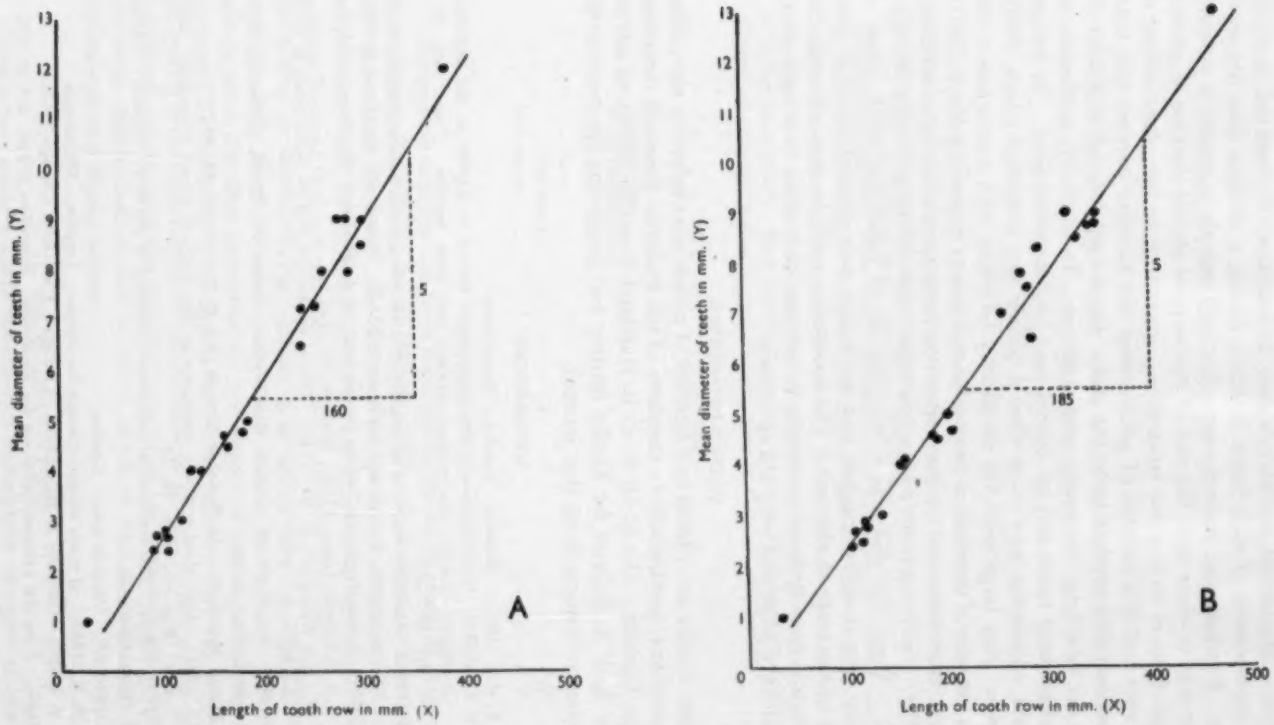

Fig. 4—Illustrations of the relationship between the length of the tooth row and the mean diameter of teeth in the row (c.f. Table).
A. Lower right tooth rows; regression coefficient=0·013; X=100, 300, when Y=2·66, 8·88.
B. Upper right tooth rows; regression coefficient=0·028; X=100, 300, when Y=2·33, 7·87.

(16 feet) crocodiles cannot, on this evidence, be less than 100 years old, in which case the replacement of each tooth 50 times during a lifetime does not seem excessive. Furthermore, since the rate of overall growth is greater in younger crocodiles than in older ones, the rate of replacement should likewise be greater in younger than it is in older crocodiles. According to the observations of Kvam (1958) and of a number of professional and amateur keepers who have been consulted, this appears to be the case. On the other hand, it is difficult to assess for how long succession may continue. In captivity, succession in old crocodiles may cease and an animal may become edentulous. In certain lizards, too, succession may cease when a certain size is reached (Gans, 1957). Nevertheless, very large crocodile skulls may be found with a complete tooth row, as in the case of the skull of *Crocodilus americanus* figured by Mook (1921). The largest skull examined by the writer was from a crocodile approximately 14 feet long. Only one tooth row (upper right) was undamaged being 490 mm. in length. Along this row was a complete set of functional teeth, some of which were very recently erupted, and successors were present below at least one third of the teeth in the row. The conclusion must be that although the rate of replacement in large crocodiles is perhaps very slow, it is only likely to cease in very large and very old specimens.

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LOCOMOTORY POWERS OF ADULT ASCIDIANS

BY

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(With 2 figures in the text)

Adults of several species of both solitary and colonial ascidians are capable of slow crawling, involving the progressive formation of new attachments and tearing or dissolving the old ones. The ampullae play a leading part. A moving colony may divide into two, or two adjacent colonies may fuse: true fusion has been observed only once, in *Trididemnum tenerum*. Both *Ciona intestinalis* and *Diplosoma listerianum* may metamorphose by attachment to the surface film and are capable of post-metamorphic attachment to a solid surface for a prolonged period. In such attachment the ampullae play a leading role. A free-swimming (unattached) colony of *Diplosoma* takes on the form of a *Pyrosoma* colony. Such colonies have been reared in the laboratory forming cigar-shaped, jet-propelled bodies up to 1 cm. long with as many as fifty zooids.

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INTRODUCTION

Locomotory activity has been reported in the adult stage of several species of ascidians, *Botrylloides leachi* (White, 1877), *Diplosoma listerianum* (Valle, 1900 a, b ; also Professor H. Munro Fox, personal communication), *Ciona intestinalis* (Valle, 1901), but little notice has been taken of these observations, perhaps because they are old observations in obscure journals. In *Botrylloides* the colony is described as moving by pseudopodia-like projections of the common test, blunt rounded projections which move by a sort of rolling action, much like that prescribed by one theory of pseudopodial movement in Amoeba (White, 1877). In *Diplosoma* Valle believed that the migrations of the colony were determined by movements of the ampullae, which pulled the individual zooids, and the attached region of the common test, after them. The same mechanism is said to serve in *Ciona* and possibly also in newly metamorphosed *Styela plicata*.

FIELD OBSERVATIONS

During two years I made monthly or fortnightly tracgins of the outlines of colonies of *Didemnum candidum*, *D. gelatinosum* and *Trididemnum tenerum*

growing on rocks on the shore in and near Plymouth. In each of these species, in addition to the extensions of the colony by growth, which occurred only at certain seasons of the year, the edge of the colony was found to retreat or to advance from time to time in various places. Some colonies, moreover, advanced in a steady direction so that in the course of three months they were up to 8 cm. away from the starting place. In one colony of *D. candidum* the two ends of the colony moved in opposite directions after a time, and the original single colony split into two separate colonies which went their own ways. On another occasion two colonies of *T. tenerum* which were near together moved towards one another and when they met fused together into a single colony ; the two were of noticeably different colour and the boundary between them remained distinct for about two months, after which time all that was noticeable was a shading from one colour at one end of the colony to the other at the opposite end. When the specimen was fixed and sectioned it was found that true fusion had occurred and the vascular channels of the common test were continuous throughout. It is possible, of course, that they originated from the splitting of a single colony and this fusion was simply the re-fusion of two separated parts of the same clone.

LABORATORY STUDIES

There can be little doubt, then, that locomotory activity is general in adult Didemnidae, and that such locomotion can lead to the fusion of colonies, or, more frequently, to the division of colonies, thus forming a kind of vegetative reproduction. Observations in the laboratory, in Plymouth and Naples, have extended the list of species in which such migration of colonies may take place. In Naples *Cystodytes dellechiajei* and *Distaplia magnilarva* have been seen to change their position on the rock to which they were attached. In Plymouth, *Botryllus schlosseri*, *Botrylloides leachi* and *Diplosoma listerianum* have been observed to migrate across the glass of aquarium tanks, where they are endemic to the fauna of the circulatory system.

Larvae of ascidians of this endemic fauna of the aquarium were selected for detailed observation of the mechanism of locomotory movements of the adults. These larvae of *Diplosoma listerianum* and *Ciona intestinalis* were obtained by using a plankton net in the reservoirs. Among them were found specimens in all stages of metamorphosis, up to the fully formed ascidiozooids. It was clear that metamorphosis had taken place in these individuals either in midwater or attached to the surface film, probably the latter since *Ciona* larvae, as shown by Willey (1893) and Berrill (1947), frequently secrete a gas bubble at the anterior end of the attachment area and float upwards to the surface. The same is true of *Diplosoma* larvae and I have frequently observed both species metamorphose by attachment to the surface film. The metamorphosed ascidiozooids taken in plankton nets in the reservoirs of Plymouth aquarium have never been attached to any solid substratum.

Ciona

When unattached individuals of *Ciona* were maintained in plunger jars in conditions preventing settling, they grew for a time in midwater, reaching a

final size of 6–7 mm. expanded overall length, never more. At this stage they had attained a single median atrial siphon, which had migrated to the anterior end from its initial position midway along ; the original six protostigmata had divided to form six double rows of about ten–twelve stigmata per half row, and the full number of muscle bands had appeared. The ascidiozooid in fact had taken on the adult form. Some of them even produced sperm in the spermducts. At this point, however, development stopped if settling was prevented, and size increase ceased ; no further rows of stigmata formed, and eggs were not produced. This stage corresponds roughly to that illustrated by Berrill (1947) in his figure 3A. Up to and including this stage settlement and attachment seem to be possible, and indeed necessary, if development is to proceed further.

In any post-metamorphic attachment of *Ciona* the epidermal ampullae play the leading part. In any small ascidiozooid of this species, whether attached or free, the ampullae may be seen pulsating ; indeed this is true of any transparent ascidian species (*vide* Valle, 1900 a). When the tip of one of these ampullae comes into contact with a surface during one of its periods of extension, it may be observed to pause in its rhythm of pulsation, and, provided no current sweeps the zooid away, the ampulla secretes at its tip some form of cement which attaches it to this surface. Meanwhile the other ampullae bend on their pedicels and expand towards the point where the first ampulla is attaching, until they too make contact with the surface. Probably the cement secreted by the ampullae is tunicin. Once the zooid is attached in this way the ampullae wander over the surface extending the area of attachment. It is in this way that migration of the whole zooid takes place. This I have observed most often as a negative phototactic response. Unilateral illumination leads to the ampullae moving away from the light source and attaching on the far side. When this continues the original attachments may be broken or dissolved, as the animal moves along. This ability to migrate seems to be lost in the mature *Ciona* and the ability to reattach seems also to disappear before 1·5 cm. expanded length is reached.

Diplosoma

In *Diplosoma*, on the other hand, mature colonies or fragments of colonies retain throughout life the ability to reattach if torn from the substratum. This is perhaps a neotenous feature, for *Diplosoma* betrays neoteny in many of its characteristics, particularly in the so-called precocious budding, which may begin in the larva, and in the small number of rows of stigmata, which it shares in common with the rest of the Didemnidae. When an unattached, newly metamorphosed *Diplosoma* colony, consisting of the oozooid and one or two blastozooids, is maintained in a plunger jar under conditions in which settling is precluded, growth may go on apparently indefinitely, while the colony remains pelagic. The characteristic encrusting form cannot of course develop if it is not growing upon a surface, and instead, as budding proceeds, first a gastrula-shaped colony is formed, around a single common cloacal cavity and a single cloacal aperture. Then, as more blastozooids are budded off, the colony takes on a cigar shape, still with a single cloacal cavity and

aperture. A colony with 50 zooids—a size of colony which if encrusting would have several cloacal apertures—has, if unattached, only a single cloacal aperture, which is sited at one end of the cigar. The general form of the colony is extremely like *Pyrosoma* under these conditions, and the same effect of jet propulsion which is seen in the swimming of a *Pyrosoma* colony is developed in such a colony of *Diplosoma*, by the combined exhalent current of many zooids directed out through a single terminal cloacal aperture.

When a post-metamorphic *Diplosoma* colony is allowed to settle, the epidermal ampullae, as in *Ciona*, play the main part in attaching the colony. The general mechanism is similar to that in *Ciona*, but complications arise from the multiplicity of zooids involved and from the colony form. If the colony consists of less than about six zooids the process of attachment is relatively simple, involving no extensive rearrangement of the colony. When, however, the colony consists of sufficient zooids for the " gastrula " or cigar-form to develop the individual zooids no longer extend through the entire

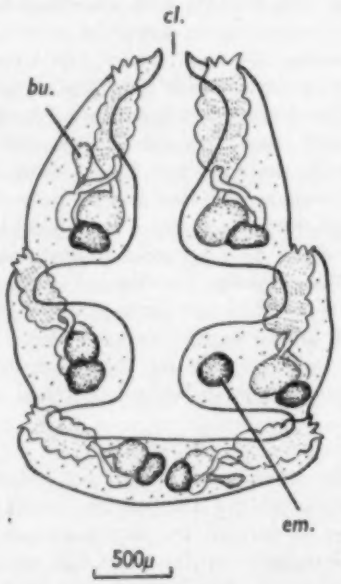

Fig. 1—An optical section through a free-swimming colony of *Diplosoma listerianum*. The colony contains 12 zooids (of which only six may be seen in the section) and only a single cloacal aperture. The stream of water from this aperture makes a swimming jet which propels the colony.
bu. bud ; *cl.* cloacal aperture ; *em.* embryo.

thickness, and any surface which may attach to the substratum is for, some of the zooids at least, the oral or upper surface of the colony. The ampullae nevertheless attach the colony so that some zooids present their oral siphons to the substratum. There then follows a rapid internal movement and

reorganization of the zooids which seem to turn about and burrow through the test substance till they come to occupy a more or less normal position. In the larger colonies this often entails regression of the thorax of some of the zooids which revolve and present a newly budded thorax to the upper surface of the now firmly attached colony. At the same time new cloacal siphons appear on the oral surface of the colony, bursting through the test substance.

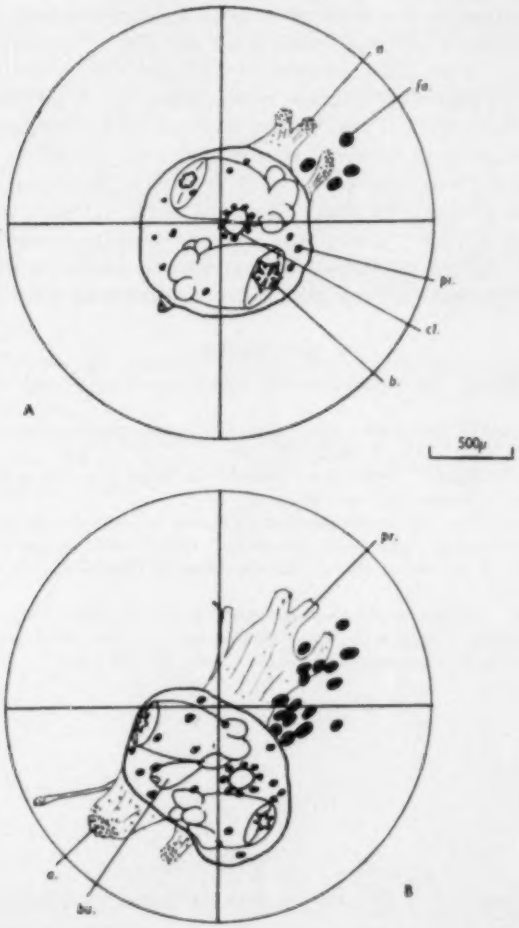

Fig. 2.—Camera lucida drawings of the position of a very young colony of *Diplosoma listerianum*. B depicts the position 12 hours after A. The colony contains only two zooids and is crawling away from the direction of fall of the faecal pellets.

a. ampulla in a process of the test with many amoebocytes (shown as dots) ; *b.* buccal aperture; *bu.* bud ; *cl.* cloacal aperture ; *fa.* faecal pellet ; *pi.* pigment cell ; *pr.* process of the test from which the ampulla has withdrawn and the amoebocytes have emigrated.

An attached colony of *Diplosoma* is surrounded by radiating processes of test substance like guy-ropes to a marquee. Each of these processes contains an ampulla and an abundant blood supply. Streaming out from the ends may be observed a regular procession of amoebocytes, which under the phase contrast microscope can be seen to be laden with granules. It seems probable that this forms a means of excretion by phagocytes which are then lost to the body. As they leave the test they drag with them a short strand of test substance, in this way extending the ' guy-rope ' by which they are leaving. Unilateral illumination seems to provoke a positive phototactic response in *Diplosoma*, if the level of illumination is not too high. Ampullae are removed from ' guy-ropes ' on the shaded side and they form fresh ones on the illuminated side. The amoebocytes all migrate to the illuminated side and choose that side to vacate the colony. This is soon followed by a movement of the whole colony towards the light source. In a similar way the colony may shun too bright light, shun heat and move away from the predominant direction in which the faecal pellets are falling. A colony of half a dozen zooids may move more than its own diameter in a day. The mechanism of locomotion appears to depend, as in *Ciona*, upon the activity of the ampullae in the ' guy-ropes ', but it is possible that the migrating amoebocytes may also help.

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NOTICE

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